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Morphological observations on the gills of dendrobranchiate shrimps

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Abstract

Gill morphology, traditionally, has played an important role in attempts to reconstruct the phylogenetic history of the Crustacea Decapoda. We examined the gills of dendrobranchiate shrimps (Crustacea, Decapoda, Dendrobranchiata) to test the assumption that all members of the clade have gills that are "dendrobranchiate" (highly branching) in form, from whence the taxon name Dendrobranchiata comes. Currently, the Dendrobranchiata consists of two superfamilies and seven families. Specimens from two genera in each of the known families were examined using light and scanning electron microscopy. Members of the family Luciferidae, all of which lack gills as adults, were not examined. Only one genus was examined for the Penaeidae (because they have been the subject of numerous previous studies) and Sicyoniidae (a monogeneric family). All gills examined have secondary branches that are further subdivided, conforming to existing and rather broad definitions of dendrobranchiate gills. Families with "typical" dendrobranchiate gills, which consist of curved secondary branches that in turn bear branched (dendritic) tubular tertiary elements on their distal surfaces, include the Penaeidae, Aristeidae, and Solenoceridae. In other families, secondary and tertiary gill elements are sometimes quite flattened, and the tertiary elements are not dendritic, giving the gill a distinctly non-dendrobranchiate appearance. Flattened biserial secondary branches and their flattened tertiary elements are particularly obvious in gills of the monogeneric family Sicyoniidae (*Sicyonia*). Within the family Sergestidae, gills of the genus *Sergestes* are unusual in having secondary branches that arise from the main gill axis in an alternating pattern; these gills also have distinctly oval tertiary elements that are not further subdivided and are directed basally rather than distally. Another sergestid genus, *Petalidium*, displays gills that differ from those of *Sergestes*; in *Petalidium* the secondary branches also come off the main gill axis in an alternating pattern, but these branches are more widely spaced and have relatively larger and broader tertiary elements when compared with gills of *Sergestes*. The family Benthesicyemidae also contains species with different gill types; *Gennadas* is shown to have flattened, plate-like tertiary elements, whereas *Benthesicyemus* has more typical dendrobranchiate gills. The significance of this variation in gill morphology within families and within the Dendrobranchiata as a whole is unclear at this point; rearrangements of the currently accepted phylogeny and resulting classification based solely on gill morphology are not recommended at this time.

Keywords: Crustacea; Decapoda; Dendrobranchiata; Gills; Morphology

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1. Introduction

In decapod crustacean systematics, there appears to be a near consensus that the penaeoid and sergestoid shrimps (the infraorder Dendrobranchiata) form the sister group to all other decapods, which collectively are often termed the Pleocyemata (see discussion in Martin and Davis 2001). The most salient characters separating the dendrobranchiates from the pleocyemates concern the carrying of eggs and the nature of their subsequent hatching: dendrobranchiates shed their eggs directly into the sea, where they hatch as naupliar larvae, whereas all other decapods (pleocyemates) carry their eggs on abdominal pleopods, with hatching occurring at a later developmental stage that is often called a zoea.

The name Pleocyemata, although not defined by Burkenroad (1963) when he proposed it, is probably from the Greek words *pleo* (swim, sail) and *cymado* (a pregnant woman, or fertile, from *kyo*, to be pregnant) (Brown 1956), and undoubtedly refers to the ability of the group to carry eggs on the swimming appendages (pleopods). The name Dendrobranchiata (from the Greek *dendron*, tree, and *branchia*, gills), coined by Bate (1888), refers to the highly branching ‘‘tree-like’’ nature of the gills.

As the choice of the name Dendrobranchiata would seem to imply, gill morphology is an important morphological character separating these two major lineages of the Decapoda. Dendrobranchiates have gills that are highly subdivided. Each gill consists of a long central axis, sometimes called the rachis, from which arises a series of paired branches (referred to here as ‘‘secondary’’ branches). These secondary branches curve slightly toward one another, creating something of a central hollow longitudinal space between them. Each branch in turn is subdivided into smaller fingerlike processes (which we are calling ‘‘tertiary’’ processes or elements) that arise from the distal surfaces of the branch, and each fingerlike process is also branched (dendritic). These gills are referred to as dendrobranchiate gills or simply ‘‘dendrobranchs.’’ Pleocyemates, on the other hand, have either gills that consist of a rachis that gives rise to paired, biserial, flattened plates that are not further subdivided (called ‘‘phyllobranchiate’’ gills or phyllobranchs) or gills that consist of unpaired processes that arise directly from the central axis and that tend to be more tubular than flattened (called ‘‘trichobranchs’’). Further discussions of gill morphology and of classifications of decapods based on gill structure can be found in the works of Burkenroad (1963, 1981, 1983), Glaessner (1969), Felgenhauer and Abele (1983), Taylor and Taylor (1992), McLay (1999), and McLaughlin et al. (2007).

Within the Pleocyemata, it is now known that there is considerable variation in gill morphology and that some taxa possess gills that do not comfortably fit within existing definitions of phyllobranch or trichobranch gills (noted in Felgenhauer (1992), see also Martin and Abele (1986) for thalassinideans and anomurans, McLay (1999) for dynomenids, and McLaughlin et al. (2007) for anomurans). In contrast, we were somewhat surprised to learn that few studies have addressed in any detail the variation in gill morphology among the Dendrobranchiata. This is particularly surprising in light of the importance placed on gill morphology at this presumably very basic level of decapod evolution. Those studies that have described dendrobranchiate gills have focused almost exclusively on the commercially important penaeoids, and usually on the genus *Penaeus* itself or on species formerly assigned to *Penaeus* (e.g. Kubo 1949; Young 1959; Foster and Howse 1978). To our knowledge, all published SEM figures of dendrobranchiate gills (e.g. Abele and Felgenhauer 1986, Fig. 9E; Felgenhauer 1992, Fig. 15A,B; Taylor and Taylor 1992, Fig. 8C,D) also have come from species of *Penaeus* (sensu latu), with the exception of some exquisite work on the gills of *Rimapenaeus* (= *Trachypenaeus*) *similis* (also in the family Penaeidae) by Bauer (1999, 2004) and some photographs of the gills of *Sicyonia parri* (family Sicyoniidae) in Bauer (1989) (Fig. 11A, unfortunately at a relatively low magnification). The only study known to us in which the gills of the Solenoceridae are described is a paper by Boschi and Angelescu (1962) on *Hymenopenaeus mülleri* (now *Pleoticus muelleri* following Pérez Farfante and Kensley 1997), and to our knowledge there are no published images of gills of the other families. Without such comparative studies, students of decapod morphology are left to assume that gill morphology within the Dendrobranchiata is more or less uniform, with all dendrobranchiate shrimps having highly branched gills similar to those of *Penaeus* (sensu latu).

Currently (following Martin and Davis (2001) which in turn relied on Pérez Farfante and Kensley (1997) for the dendrobranchiates), the Dendrobranchiata is divided into two superfamilies: the Penaeoidea containing five families, and the Sergestoidea containing only the families Luciferidae and Sergestidae. We briefly examined gill morphology in representatives of all extant dendrobranchiate families exclusive of the luciferids, which lack gills (and many other characters that might serve to place them firmly within the Dendrobranchiata) as adults, to examine the assumption that all families of dendrobranchiate shrimp possess morphologically similar gills.

2. Materials and methods

All shrimp specimens used in this study are in the Crustacea collections of the Natural History Museum of

Los Angeles County (Table 1). Two genera were examined for each dendrobranchiate family, with the exception of the families Penaeidae (because they have been the subject of most studies on dendrobranchiate gills to date, and are thus better known), Sicyonidae (because it is a monogeneric family), and Luciferidae (all of which lack gills as adults). We made an effort to use gills that were "comparable" by removing the external-most (lateral-most) gill (the arthrobranch) of the third or fourth pereiopod. In very small specimens, it was sometimes difficult to determine if the gill removed was the arthrobranch or the corresponding pleurobranch. However, as our interest was with morphology rather than gill placement, this is not a major concern.

Table 1. Specimens of dendrobranchiate shrimps examined in this study (higher level classification following Martin and Davis 2001)

Infraorder Dendrobranchiata Bate 1888
Superfamily Penaeiodea Rafinesque, 1815
Family Aristeidae Wood-Mason, 1891
Aristeus antillensis Edwards and Bouvier, 1909 (LACM CR 1986-431.1, Gulf of Mexico, off Alabama)
Aristaeopsis edwardsiana (Johnson, 1867) (LACM CR 1957-275.1, Gulf of Mexico)
Family Benthesicyemidae Wood-Mason, 1891
Gennadas propinquis Rathbun, 1906 (LACM CR 1965-098.1, Isla Guadalupe, Mexico)
Benthesicymus altus Bate, 1881 (LACM CR 1958-296.1, Salina Cruz, Mexico)
Family Penaeidae Rafinesque, 1815
Farfantepenaeus californiensis (Holmes, 1900) (LACM CR 1971-004.1, Baja California, Mexico)
Family Sicyoniidae Ortmann, 1898
Sicyonia ingentis (Burkenroad, 1938) (LACM CR 1971-005.1, Baja California, Mexico)
Family Solenoceridae Wood-Mason, 1891
Pleoticus robustus (Smith, 1885) (LACM CR 1959-302.1, Gulf of Mexico)
Solenocera vioscai (Burkenroad, 1934) (LACM CR 1956-092.1, Gulf of Mexico)
Superfamily Sergestoidea Dana, 1852
Family Luciferidae De Haan, 1849 (none examined; lack gills as adults)
Family Sergestidae Dana, 1852
Sergestes similis (Hansen, 1903) (LACM CR 1962-240.1 and LACM CR 1965-100.1, both from Santa Catalina Island, Southern California)
Petalidium suspiriosum (Burkenroad, 1937) (LACM CR 1966-349.2, Southern California)

LACM CR refers to catalog numbers in the Crustacea collections of the Natural History Museum of Los Angeles County.

Preparation for SEM included hydration of the gill tissue to pure water by way of a graded ethanol series, brief sonication using a light surfactant and a commercial sonicator, rehydration in an ethanol ladder to 100% ethanol, and drying in HMDS (hexamethyldisilazane). Dried specimens were mounted either on stubs or on coins using carbon tape and were viewed and photographed with a Hitachi model S-3000N scanning electron microscope.

3. Results

3.1. Infraorder Dendrobranchiata Bate, 1888

Superfamily Penaeiodea Rafinesque, 1815

3.1.1. Family Aristeidae Wood-Mason, 1891

The gills of aristeids, based on our examination of *Aristeus antillensis* Edwards and Bouvier, 1909 (Fig. 1A,B) and *Aristaeopsis edwardsiana* (Johnson, 1867) (formerly *Plesiopenaeus edwardsianus*; see Pérez Farfante and Kensley 1997) (Fig. 1C,D), are "classical" dendrobranchiate gills, with a long central axis giving rise to paired branches that curve outward from the axis and then meet again at their tips, creating a central longitudinal hollow space within the secondary branches (Fig. 1A,C). From the distal (or "upward") surface of each secondary branch arise short, branching tertiary processes that are tube-shaped and terminally rounded or blunt (Fig. 1B,D). These tertiary processes vary slightly in length, with those closer to the tips of the secondary branches usually being shorter than those arising closer to the main gill axis. Toward the tip of the gill, the secondary branches fail to completely encircle the gill, leaving the central axis somewhat exposed from a lateral viewpoint (Fig. 1A,C).

3.1.2. Family Benthesicyemidae Wood-Mason, 1891

The gills of the family Benthesicyemidae, based on our observations of *Gennadas propinquis* Rathbun, 1906 (Fig. 2A,B) and *Benthesicymus altus* Bate, 1881 (Fig. 2C,D), display morphological differences not only from other dendrobranchiate families but also from one another. The gills of *Gennadas* consist of paired secondary branches that arise from a central axis, but the branches do not curve medially to create a central longitudinal hollow space as described above. Furthermore, the tertiary elements that arise from these branches are much more flattened and have the overall appearance of "book gills" as opposed to the highly branching dendrobranchiate gill pattern described above for aristeids. Although some flattening of these gill elements could be attributed to shrinkage or deformation during our preparation of the gills for

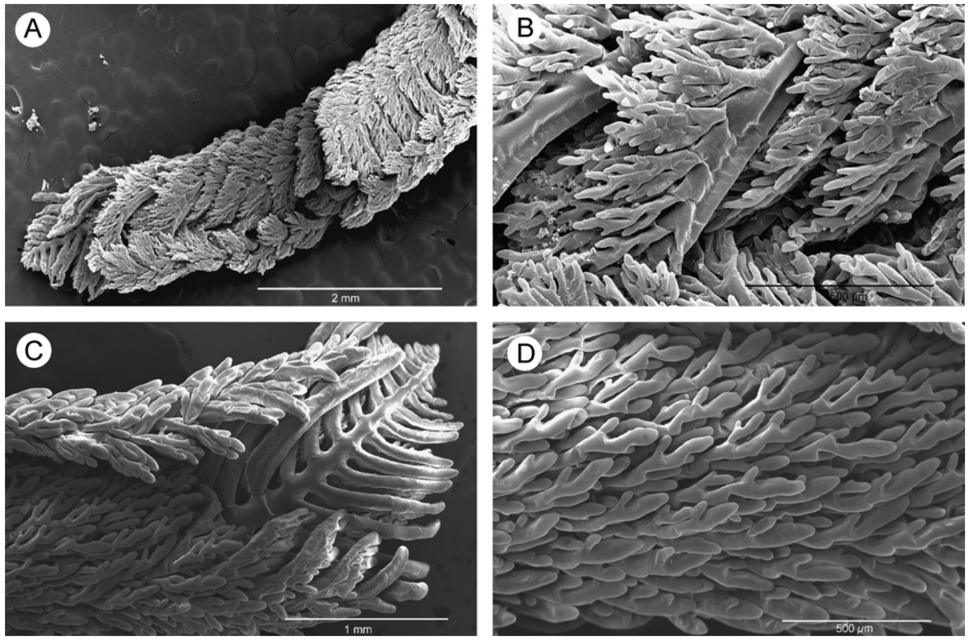

Fig. 1. Gill morphology in selected members of the family Aristeidae. (A, B), *Aristeus antillensis* Edwards and Bouvier, 1909 (LACM CR 1986-431.1). (A) View of entire pleurobranch gill (minus the base) showing how the curved secondary branches meet along the midline except at the tip of the gill, which is to the lower left. (B) Higher magnification of same gill shown in (A), with midline (where secondary branches meet) running horizontally along the lower 1/4 of the image and with highly dendritic tertiary gill elements arising from the dorsal surface (to the left) of each secondary gill branch, one of which is in the center of the photograph running diagonally from lower left to upper right. (C, D), *Aristaeopsis edwardsiana* (Johnson, 1867) (LACM CR 1957-275.1). (C) Distal end of entire gill showing curved secondary gill branches (lower left) and distal area where they fail to meet along the midline, exposing the central gill axis and its paired secondary branches. (D) Higher magnification of tertiary dendritic processes arising from the secondary branches; these processes are so dense in this view that the secondary branches themselves are obscured.

SEM observations, there is no doubt that the basic gill morphology is quite different from what was seen (above) for aristeids and other shrimp that display the more "classic" dendrobranchiate gill morphology. In contrast, the genus *Benthesicyemus* has gills that are slightly more traditional, with a central axis giving rise to branches that in turn have dorsal dendritic processes. But here, too, slight differences are apparent. The secondary branches themselves are sometimes branched at the tip (Fig. 2C, with secondary branches on the top side of the photograph), and the tertiary elements appear to branch less often (Fig. 2D) and appear overall less "dendritic" than the gills of aristeids.

3.1.3. Family Penaeidae Rafinesque, 1815

Gills of the family Penaeidae, based on our examination of *Farfantepenaeus californiensis* (Holmes, 1900) (Fig. 3A,B), display the classical dendrobranchiate gill morphology, as described above for the Aristeidae and as noted in earlier morphological studies on *Penaeus* and other genera of the family (e.g. Young 1959 for *Penaeus* (now *Litopenaeus*) *setiferus* and Foster and Howse 1978 for *Penaeus* (now *Farfantepenaeus*) *aztecus*). For penaeids, this type of gill is perhaps best illustrated in Bauer's (1999) study of *Trachypenaeus (*as *Rimapenaeus) similis*. The long central axis, paired and slightly curving secondary branches, and highly branching tertiary gill elements are all present in pleurobranchs (Fig. 3A shows two pleurobranchs arising from the body wall) and arthrobranchs (Fig. 3A,B).

3.1.4. Family Sicyoniidae Ortmann, 1898

Gills of the family Sicyoniidae, based on our examination of *Sicyonia ingentis* (Burkenroad, 1938) (Fig. 4A–D), are dramatically different from the classical dendrobranchiate gill pattern. Although paired branches arise from a central axis (Fig. 4A) and create a central longitudinal hollow space, these secondary branches are extremely flattened and plate-like, a condition that is particularly obvious when the overall gill is viewed from below (Fig. 4D). Tertiary elements arising from these secondary branches are also very flattened and show none of the "dendritic" branching seen in the tertiary process of "classic" dendrobranchiate gills. These flattened tertiary processes arise at very regular intervals along the dorsal (distal) surface of each secondary branch, creating a pattern of regular spacing that is particularly obvious at the base of the processes when viewed from the side (Fig. 4B,C). Because the genus *Sicyonia* is the only genus in the family

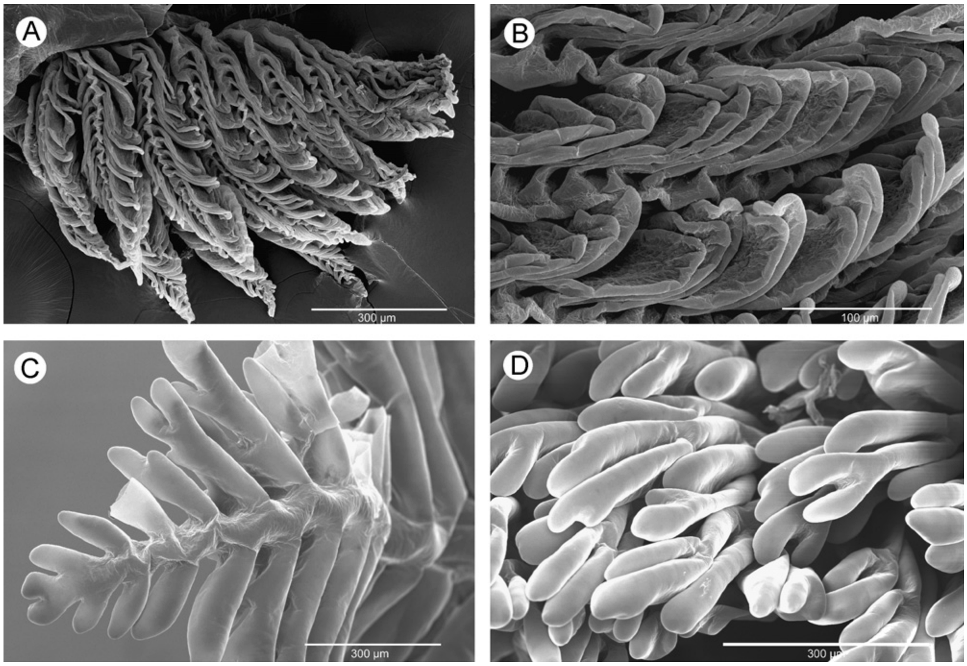

Fig. 2. Gill morphology in selected members of the family Benthesicyemidae. (A, B) *Gennadas propinquis* Rathbun, 1906 (LACM CR 1965-098.1). (A) Entire pleurobranch gill, posterior view, with point of attachment to body at upper left and with approximately 8 ''secondary branches'' shown, each with dorsal (distal) side to right bearing curved, flattened tertiary gill elements. (B) Higher magnification of gill shown in (A), with two secondary gill branches (plus parts of others at top and bottom of photograph), each bearing flattened tertiary gill elements; this image is turned 90° counterclockwise from orientation in (A). (C, D) *Benthesicymus altus* Bate, 1881 (LACM CR 1958-296.1). (C) Distalmost tip of ''rachis'' (central gill axis) (at lower left in photograph) and several paired secondary gill branches, some of which are distally bifurcated. (D) Same gill as in (C), but different orientation and higher magnification, showing tubular and branching tertiary gill elements.

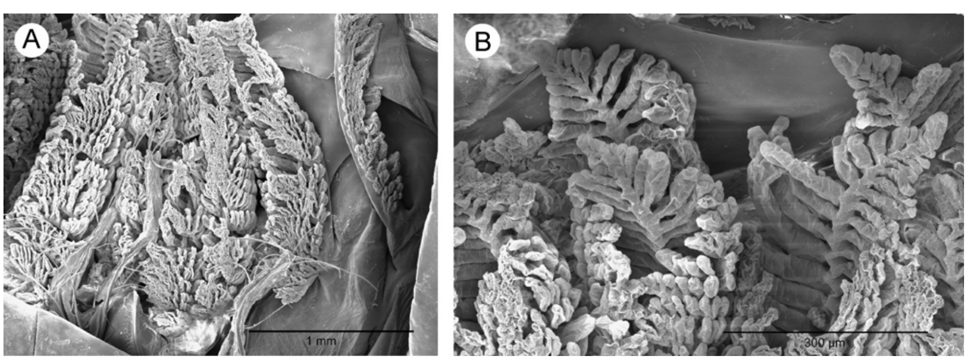

Fig. 3. Gill morphology in a species of the family Penaeidae (*Farfantepenaeus*). (A, B) *Farfantepenaeus californiensis* (Holmes, 1900) (LACM CR 1971-004.1). (A) Relatively low magnification view of several pleurobranch gills shown in posterior view, with dorsal side of specimen at top of photograph and anterior to the left. Note the attachment to the body wall of one pleurobranch gill directly over the center of the scale bar; another pleurobranch can be seen attached to the body wall just posterior to this (far right in photograph). (B) Higher magnification of gills shown in (A), in more lateral view, with tips of 4–6 gills present; gill at center left shows typical curving of secondary branches to form ''hollow'' space just basal to tip of gill and continuing basally.

Sicyonidae, no other representatives of the family were examined.

3.1.5. Family Solenoceridae Wood-Mason, 1891

The gills of solenocerids, based on our study of *Solenocera vioscai* Burkenroad, 1934 (Fig. 5A,B) and *Pleoticus robustus* (Smith, 1885) (Fig. 5C,D), are basically in keeping with our description of ''classical'' dendrobranchiate gills (as in the Aristeidae, above). Gills of *Pleoticus* in particular are essentially identical to the gills of the Aristeidae and Penaeidae, with a long central axis that gives rise to secondary branches, each of which bears numerous tubular and highly branching tertiary gill elements (Fig. 5C,D). The gills of *Solenocera*

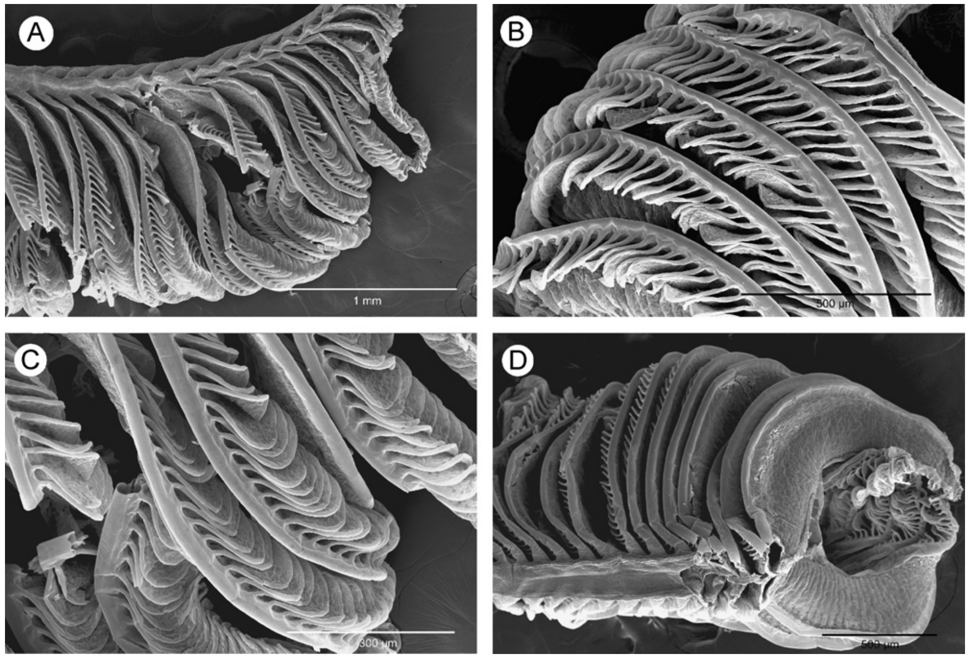

Fig. 4. Gill morphology in a species of the family Sicyonidae (*Sicyonia*). (A, B, C, D) *Sicyonia ingentis* (Burkenroad, 1938) (LACM CR 1971-005.1). (A) Nearly entire gill viewed from either the front or the back to expose main axis (rachis) at top of photograph; point of attachment to body at far left, gill tip to upper right, with secondary branches directed toward bottom of photograph. (B) Slightly higher magnification of gill shown in (A), orientation approximately 180° such that gill rachis is toward bottom of figure. (C) Higher magnification of gill showing even spacing of flattened tertiary elements; gill axis is toward top of the photograph; secondary branch at far left broken showing thin cuticle. (D) Entire gill seen from below showing plate-like nature of paired secondary branches; the main gill axis can be seen in posterior view extending horizontally toward the left of the photograph.

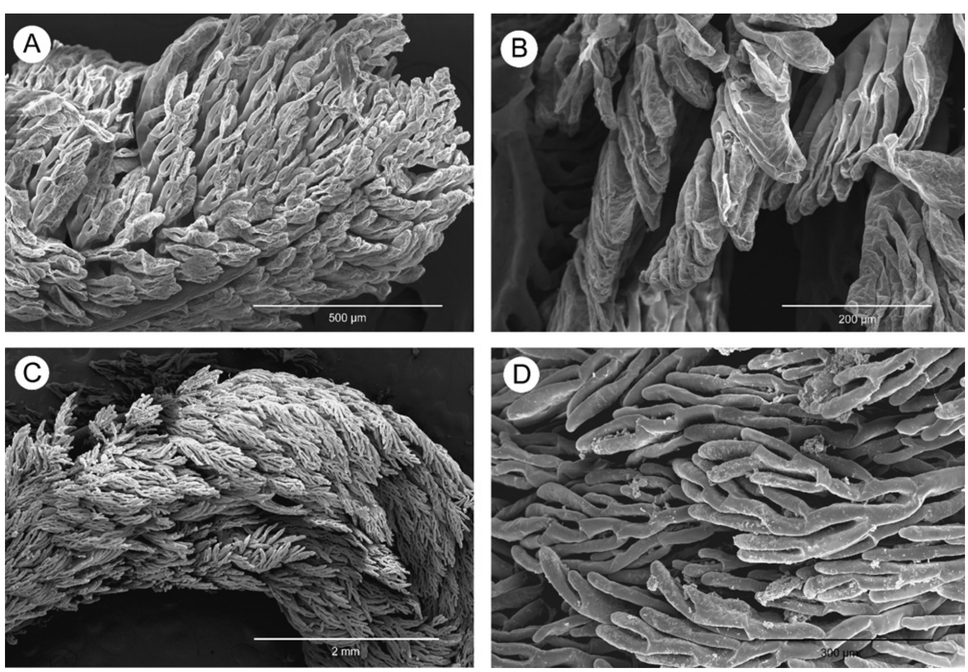

Fig. 5. Gill morphology in selected members of the family Solenoceridae. (A, B) *Solenocera vioscai* Burkenroad, 1934 (LACM CR 1956-092.1). (A) Distal extremity of entire gill, with central axis (rachis) visible running from lower left to upper right. (B) Higher magnification of tertiary gill elements, which are slightly flattened and bifurcated (especially visible at upper right in the photograph). Wrinkled cuticle is caused by drying for SEM preparation and might explain flattening to some degree. (C, D) *Pleoticus robustus* (Smith, 1885) (LACM CR 1959-302.1). (C) Approximate middle 4/5 of entire gill, with base toward lower left and tip toward lower right. (D) Higher magnification of tubular and branched tertiary elements.

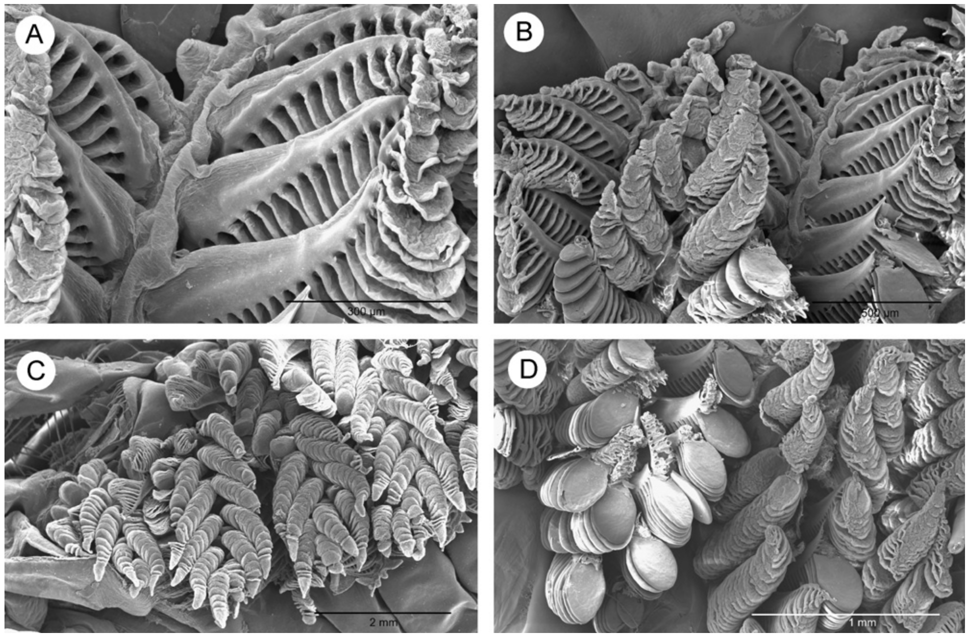

Fig. 6. Gill morphology in a species of the family Sergestidae (*Sergestes*). (A, B, C, D) *Sergestes similis* Hansen, 1903 (either LACM CR 1962-240.1 or LACM CR 1965-100.1). (A) Distal third to half of entire gill showing central gill axis (rachis) with secondary branches arising in alternating pattern; this gill is the same as in the far right in (B). (B) Distal half (approximately) of three gills, central one oriented such that secondary branches are coming toward the viewer and displaying plate-like oval, tertiary elements. (C) Low magnification view of entire field of pleurobranch gills, with approximately four entire gills shown; alternating pattern of secondary branches clearly visible in two center-most gills; orientation is 180° from the photograph in (B). (D) Series of broken secondary branches (most of which belong to a single gill) showing the individual oval plate-like tertiary elements.

are basically similar (Fig. 5A shows the main gill axis at the bottom center of the photograph, with curved branches visible directly over it and arising from it; the distal tip of the gill is to the upper right in that image). However, there appears to be some flattening of the tertiary elements (Fig. 5B). These tertiary elements are indeed branched (Fig. 5B, upper right), as in true dendrobranchiate gills, and they are not at all like the clearly defined and regularly spaced tertiary plates seen in sicyoniids (compare with Fig. 4) or the well-defined oval plates seen in the sergestoid genus *Sergestes* (below, Fig. 6). However, the distal branches of these tertiary elements are slightly flattened, and they appear to be closely appressed, more so than in "classic" dendrobranchs (e.g. compare with Fig. 5D). It is possible that some of this flattening is an artifact of our SEM preparation, as these gills also appear slightly wrinkled, but the width of the tertiary elements would seem to argue against their ever having been tubular and dendritic.

3.2. Superfamily Sergestoidea Dana, 1852

3.2.1. Family Sergestidae Dana, 1852

Gill morphology in the family Sergestidae is apparently highly variable, based on our examination of the gills of *Sergestes similis* Hansen, 1903 (Fig. 6) and *Petalidium suspiriosum* Burkenroad, 1937 (Fig. 7). In *Sergestes*, the type genus of the family, the secondary branches appear to arise in an alternating (rather than perfectly paired) pattern from the main gill axis, and they are wider basally than they are distally (Fig. 6A,B). The tertiary elements that arise from these branches are not tube-like and dendritic, but instead are flattened, oval plates (Fig. 6C,D). These plates diminish in size with distance from the main gill axis, giving the overall gill a distinctive "leaf-like" appearance (Fig. 6B,C). Furthermore, these oval plates are directed basally, toward the pereiopods (Fig. 6B,C). Gills of the genus *Petalidium* (Fig. 7) also consist of flattened secondary branches that arise from the central axis and that also give rise to flattened tertiary elements. But in *Petalidium*, the tertiary elements are not as regularly oval in shape (compare *Sergestes* in Fig. 6D with *Petalidium* in Fig. 7C and D).

3.2.2. Family Luciferidae De Haan, 1849

Members of the only other family of sergestoid shrimps, Luciferidae De Haan, 1849, all lack gills as adults, and indeed they lack many of the other morphological characters that would seem to allow their firm placement with the Dendrobranchiata. Thus, they were not included in our study.

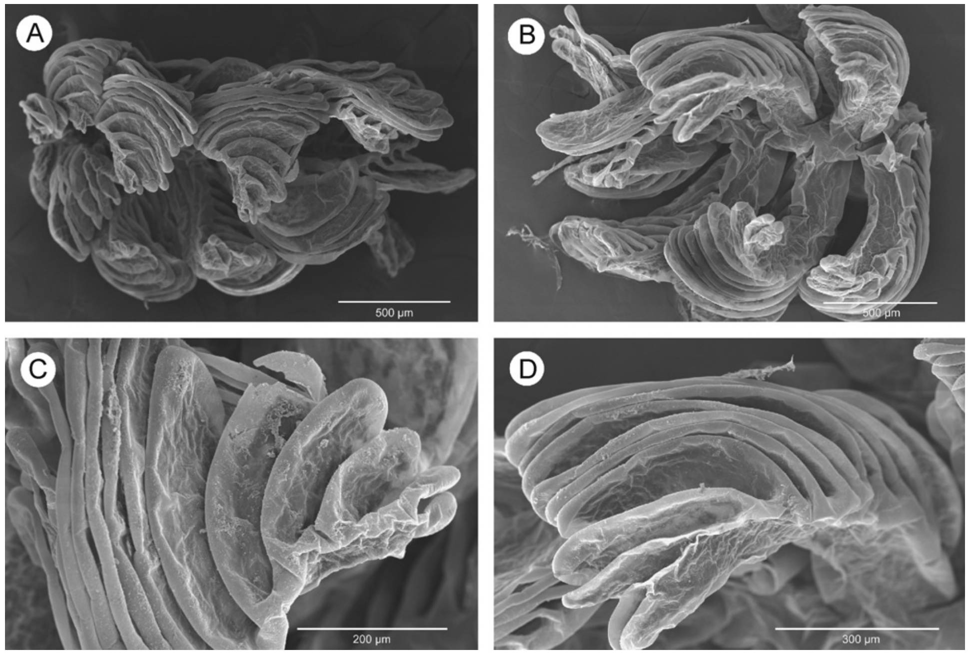

Fig. 7. Gill morphology in a species of the family Sergestidae (*Petalidium*). (A, B, C, D) *Petalidium suspiriosum* Burkenroad, 1937 (LACM CR 1966-349.2). (A) Entire gill with base toward left. (B) Slightly higher magnification of different gill showing widely spaced secondary branches and flattened, wide tertiary elements. (C) Close up photograph of a single secondary branch showing flattened and evenly spaced distal tertiary elements; tip of secondary branch is at far right in photograph. (D) Similar view showing overlapping and distal rounding of the tertiary elements.

4. Discussion

It is obvious that the "classic" dendrobranchiate gill-type, consisting of small, dendritic processes or filaments arising from curved, tubular, paired branches stemming from a long central axis (schematically depicted in Fig. 8A,B), is not found in all members of the Dendrobranchiata. We found "classic" dendrobranchiate gills only in representatives of the families Penaeidae (which is not surprising, as these are the species whose gills have been documented often in the literature), Aristeidae, and some members of the Solenoceridae (the genus *Pleoticus*) and Benthesicyemidae (genus *Benthesicyemus*, but see remarks on its morphology above). More "platelike" gill elements are found in the families Benthesicyemidae (the genus *Gennadas* in particular) and Sicyoniidae. In the Sicyoniidae, the lateral (secondary) gill branches are so flattened and plate-like that if the gills are viewed from below, it would be quite easy to mistake them for phyllobranchs (Figs. 4D,8E,F). Sergestids, which are members of the other dendrobranchiate superfamily, appear somewhat intermediate, with a basically tree-like structure to the main gill axis and secondary branches, but with flattened dorsal tertiary projections arising from each branch (more obvious in *Sergestes*, Fig. 6, than in *Petalidium*, Fig. 7). Additionally, the secondary branches of the sergestid gill appear to come off the main stem (rachis) in an alternating pattern, rather than being evenly paired as is seen in the penaeoid-like gills, and the tertiary plate-like elements appear to be directed outward (laterally) and downward more than distally (see Figs. 6A–C, 8C,D for *Sergestes*). The gills of *Petalidium* (Fig. 7) are not quite as dramatically different from "classic" penaeoid gills as are those of *Sergestes*, possibly because these shrimp (and thus their gills) are much smaller to begin with, but the tertiary elements of the gills of *Petalidium* are clearly plate-like rather than being tubular and highly branched.

Despite the variation we have documented here, all of these gills are nevertheless still "dendrobranchiate" gills, especially if we apply the more general description of such gills given by Barnes and Harrison (1992): "dendrobranchiate [gills have] evaginations (foldings) from the central gill axis [that] are subbranched," as compared with gills of the Pleocyemata in which "evaginations from the central gill axis are not subbranched." By this broad definition, all the gills examined by us fall under the "dendrobranchiate" heading, as they all consist of paired branches that are secondarily subdivided, albeit in different ways (Fig. 8). The slightly more restrictive definition of dendrobranchiate gills given by Young (1959) (in turn based on Calman 1909) also applies, more or less, to all gills examined here: "This type of gill is comprised [sic] of a primary axis or rachis from which pairs of secondary structures bearing gill filaments arise at right angles" (Young 1959, p.149).

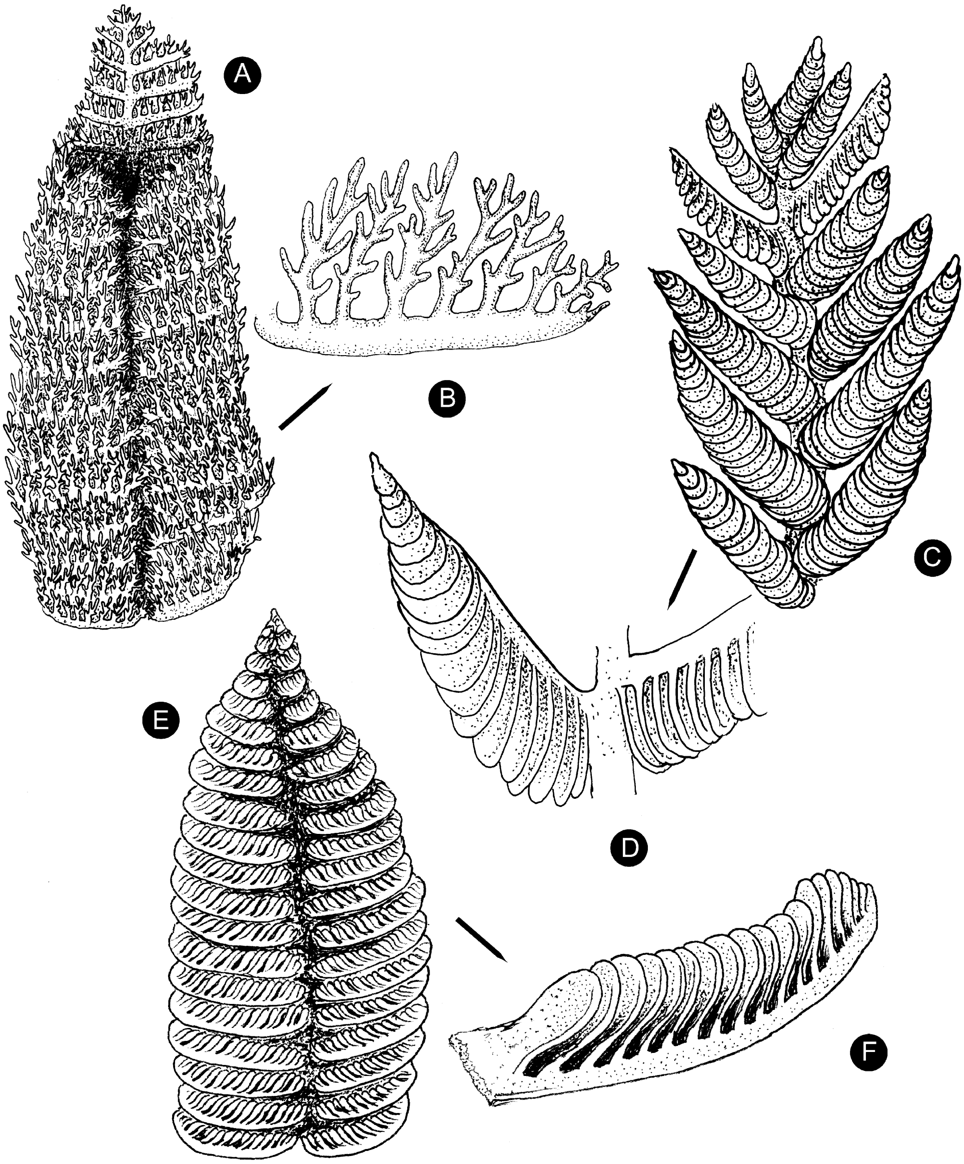

Fig. 8. Schematic illustrations of some of the more extreme variations seen among "dendrobranchiate" gills. (A) The "classical" dendrobranchiate gill found in penaeids, aristeids, and at least some benthesicyemids and solenocerids, seen in lateral view, with secondary arms curving off the main gill axis toward the viewer and meeting at the midline. (B) Part of a single secondary gill branch of the gill type shown in (A), with tubular, dendritic tertiary gill elements directed distally. (C) The gill of the sergestid genus *Sergestes* in lateral view, with secondary branches arising in an alternating pattern off the main gill axis and with flattened, oval tertiary elements directed laterally and basally. (D) Parts of two secondary gill branches coming off the main gill axis in the *Sergestes* gill, with each branch bearing flattened, oval tertiary elements. (E) The "plate-like" dendrobranchiate gills of the Sicyoniidae (*Sicyonia*) in lateral view. (F) Distal part of a single secondary branch of the sicyoniid gill showing a flattened secondary gill branch giving rise to flattened tertiary elements directed distally. Not drawn to scale.

Yet the details of the gills in the six families we examined are more different from one another than we had anticipated. If we were to group the families on the basis of gill morphology alone, the families Penaeidae, Aristeidae, and Solenoceridae, with their more "traditional" dendrobranchiate gill morphologies, would appear more closely related to one another, and the families Sicyoniidae, Benthesicyemidae, and Sergestidae, with their more plate-like gills, perhaps could be seen as constituting a separate clade. The very unusual and distinctive gill of the genus *Sicyonia* (family Sicyoniidae) is similar in some ways to what is seen in *Gennadas* (Fig. 2A,B, family Benthesicyemidae) and in *Petalidium* (Fig. 7, family Sergestidae), but it is not like the other benthesicyemid we examined (genus *Benthesicyemus*). Differing even further from the classic dendrobranchiate gill morphology is the gill of the sergestid genus *Sergestes* (Figs. 6,8C,D), with its unusual alternating arrangement of branches and distinctive oval plates for tertiary elements; the flattened tertiary elements again are quite similar to what is seen in the Sicyoniidae. However, grouping sicyoniids with sergestids is of course in contrast to currently accepted classifications of the Dendrobranchiata.

The Sergestidae appear in some ways intermediate in their gill morphology between the plate-like gills of the sicyoniids and the gills of other dendrobranchiates, with plate-like tertiary processes arising from each branch but without the secondary branches themselves being flattened. The flattening of the gill elements in sergestids seems to us more similar to what is seen in the sicyoniids and also in *Gennadas* (in the Benthesicyemidae) than it is to the "penaeoid" condition. Solenocerids also are somewhat intermediate, given the slight flattening of the tertiary elements seen in the genus *Solenocera* (Fig. 5B, but see also our caveat about SEM preparation techniques and the possibility of the *Solenocera* gill appearing unnaturally flattened as a result). It seems likely that the flattening of the secondary and/or tertiary branches has evolved independently in several dendrobranchiate lineages, and we are not proposing any changes in the current classification of the dendrobranchiates based on gill morphology at this time. Our working hypothesis is that the highly branching "penaeoid" form of the dendrobranchiate gill (schematically represented in Fig. 8A,B) is the more plesiomorphic gill within the Dendrobranchiata, and that the various modifications might have arisen later by a flattening of the tertiary gill elements (as in the sergestids) or a flattening of the entire lateral secondary gill branches (as in the sicyoniids). This view is consistent with Burkenroad's (1983, p.285) suggestion that the sicyoniids may have arisen via paedogenesis from a *Penaeus*-like ancestor.

Given the incredible diversity of the decapods, it should come as no surprise to learn that the earlier and somewhat simplistic view of decapods having three, and only three, morphological gill types (Abele and Felgenhauer 1986) is an overgeneralization. Descriptions of gills that do not comfortably conform to previous descriptions of decapod gill types have been mentioned by Martin and Abele (1986) for anomurans and thalassinoids, McLay (1999) for dynomenid crabs, McLaughlin et al. (2007) for anomurans, and others. For example, within a single family of crabs, the Dynomenidae, McLay (1999) noted that "we have gills ranging from the multilobed trichobranchiate-like condition seen in *Hirsutodyomene* …through *D. hispida* and *D. praedator,* in which the number of lobes is reduced to only two (which are flattened) and finally the phyllobranchiate-like condition seen in *Acanthodromia*."

Readers should not assume that all members of the dendrobranchiate families examined here have gills that conform to the gill morphology of species we examined and illustrated. Our review must be considered cursory in that we examined only two genera in most families (excluding the previously studied Penaeidae, the monogeneric Sicyoniidae, and the gill-less Luciferidae). There may be additional and significant variation within families that is equal to, or that exceeds, the differences we have noted among families based on these few representatives. Our point here is simply to note that the "classic" dendrobranchiate gill condition is not universally shared among the families currently treated as the Dendrobranchiata.

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