Dexaminoidea of the NEP (Equator to Aleutians, intertidal to abyss): a review. Donald B. Cadien 22 July 2004 (revised 21 Sept 2007)

Introduction to the Dexaminoidea

The superfamily was created by Bousfield (1979) when he first conceptualized the general structural division and organization of the non-gammaroids (those amphipods not fitting into the traditional concept of the Gammaridae s.l.). The concept has not changed since that time (Bousfield 1982, Bousfield and Shih, 1994, Bousfield 2001).

He viewed the component families as Atylidae, Anatylidae, Dexaminidae, Lepechinellidae, and Prophliantidae. This view is not held by many others, including J. L. Barnard, who in 1970 coalesced all of these families under the Dexaminidae. Only one of these groups (the Prophliantidae) was even accorded subfamilial status in Barnard and Karaman (1991). Their decision has been followed by McLaughlin et al (2005) who list all NEP dexaminoids as within the Dexaminidae. Bousfield and Kendall (1994) still maintained the Atylidae (with subfamilies Atylinae, Lepechinellinae, Nototropiinae, and Anatylinae) and Dexaminidae (with subfamilies Dexamininae, Polycheriinae, Dexaminoculinae, and Prophliantinae) as valid. We follow McLaughlin et al (2005) in uniting these two groups as Dexaminidae, the single family within the superfamily Dexaminoidea, as is the related Ampeliscidae the only family in the Ampeliscoidea.

The group has received some attention in the NEP, with review papers by J. L. Barnard (1970, 1973) and Bousfield and Kendall (1994). Hirayama has also published a series of papers (1983, 1984, 1985, and 1986) on the related dexaminoid fauna of the northwest Pacific

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Dexamine thea from the North Atlantic (photo Cedric d'Udekem d'Acoz)

Diagnosis of the Dexaminoidea

"Plesiomorphic, rostrate, and abdominally carinate, nestling and fossorial marine gammarideans, having a dimorphic pelagic terminal male stage; peduncles of antennae 1 and/or 2 bear brush setae, but lack calceoli; antenna 2 peduncle elongate; accessory flagellum lacking (occasionally vestigial); eyes reniform or rounded, lateral; mouthparts somewhat modified; upper lip, apical margin slightly incised; lower lip inner lobes variously (usually strongly) developed; mandibular molar strong, palp normal (or lacking); inner plates of maxillae weakly setose; outer plate of maxilla 1 with 11 apical spine teeth; maxilliped plates normal, palp reduced; coxal plates medium to deep, 4th excavate; coxae 5-7 equi- or anteriorly lobate; gnathopods 1 and 2 weakly amplexing, subsimilar, subcheate; peraeopods 5-7 heteropodous, bases various; brood plates medium broad; some coxal gills pleated or foliaceous, present on peraeopod 7; pleopods normal; urosome segments 5 and 6 coalesced; uropods lanceolate, rami of 2 unequal; uroppod 3 foliaceous, outer ramus 1-segmented; telson lobes deeply and narrowly separated, apices with shallow notch and spine." (Bousfield 1979).

Ecological Commentary

Most, if not all, shallow-water dexaminoids are epifaunal animals normally found associated with either algae (J. L. Barnard 1972b) or with other invertebrates. J. L. Barnard (1972a) suggests that they are similar ecologically to the pleustids, but radiated primarily in the southern rather than in the northern hemisphere. In California Polycheria osborni is a well-known associate of tunicates (Skogsberg and Vansell 1928), which it uses to construct temporary domiciles by forming the flesh of a compound tunicate around it with its prehensile legs. Within the groove created the animal lives and filterfeeds for suspended particulates. Personal observations of the same species off San Onofre have seen similar behavior with regard to sponges. There, however, the amphipods creat excavations within the surface of the sponge within which they live. They may filter feed here as well, but the infiltration of the cavity by mesenchymal cells from the sponge suggests that these may also be ingested by the amphipod. This would then be a case of microcarnivory rather than a simple commensal association. Polycheria antarctica is listed as associated with both sponge and ascidian hosts in Antarctica (De Brover et al. 2001). At least one other member of the genus Polycheria is known from sponge hosts in British Columbia, where *P. mixillae* is described as a commensal with the demosponge Myxilla incrustans (Bousfield and Kendall 1994). Since all members of the genus have similar pincher-like prehensile legs, it is assumed that they all are associated with hosts, only a few of which are currently known.

Deeper dwelling dexaminoids such as *Guernea* and *Lepechinella* probably do not share associations with other organisms. This is reflected in their legs, which do not bear prehensile dactyls as do the algal and invertebrate associated forms. Lepechinella all have more elongate simple or slightly curved dactyls useful for standing on soft bottoms rather than clutching host structure (see J. L. Barnard 1973). The same is true of *Guernea* (J. L. Barnard 1958, 1970). The atylids appear to be somewhat intermediate, living in shallow well lit bottoms, but not in direct association with other organisms. They are described as slow-moving nestlers and cavity dwellers who harvest surface particulates from soft bottoms (Bousfield and Kendall 1994). J. L. Barnard reports mixtures of sediment particles and organic material in the gut of *Lepichinella pangola* (J. L. Barnard 1962), so similar feeding styles may prevail for at least a portion of the deeper living dexaminoids.

Key to NEP Dexaminoid genera

The recent treatment of Bousfield and Kendall (1994) covers most of these species. While their concept of the family differs in that they would subdivide it more finely than seems acceptable to others, this very fact has lead to their provision of keys to the subfamilies of the Atylinae (p. 8) and Dexamininae (p. 36) which, combined cover the taxa viewed here as comprising the Dexaminidae. Following their subdivisions (for convenience in use of their paper) species of *Atylus* would be found in the Atylinae, species of Lepechinella in the Lepechinellinae, species of Guernea in the Prophliantinae, species of *Paradexamine* in the Dexamininae, and species of *Polycheria* in the Polycheriinae. While their keys have some of the same problems encountered in others from this series, they appear generally serviceable and interpretable. I recommend you at least try them. Generic keys are provided for the genera Atylus and Polycheria, which have multiple species in the NEP, but not for the remaining genera of dexaminids. The treatment of Lepechinella is particularly cavalier in their paper, apparently because the collections they were examining did not contain representatives of this genus. An alternative key to genera of Dexaminidae, which includes all five of the genera known from the NEP is provided in Ledoyer (1982, p. 328, don't worry the key is in both French and English!).

NEP Dexaminoidea based on McLaughlin et al (2005) augmented by known provisional species. *=Taxa on the SCAMIT Ed. 4 list. Valid taxa are **bolded**, synonyms are not

Family Dexaminidae

Atylus atlassovi (Gurjanova 1951) – Sea of Okhotsk to Aleutian Ids.; shallow Atylus borealis Bousfield and Kendall 1994 – SE Alaska to Strait of Juan de Fuca: 0-10m Atylus brueggeni (Gurjanova 1938) – Sea of Japan to Aleutian Ids.; 10-80m Atvlus carinatus (J. C. Fabricius 1793) - Arctic Alaska; 0-50m Atylus collingi (Gurjanova 1938) – Japan Sea to Puget Sound; 3-10m Atylus georgianus Bousfield and Kendall 1994 – Queen Charlotte Ids. to Oregon; 0-3m Atylus laevidensis J. L. Barnard 1956 - SE Alaska to Central California; 0-2m *Atylus tridens (Alderman 1936) – Queen Charlotte Ids to La Jolla; 0-135m Dexamonica reduncans J. L. Barnard 1958 (=Guernea reduncans) Gammarus carinatus J. C. Fabricius 1793 (= Atylus carinatus) *Guernea reduncans (J. L. Barnard 1958) – Queen Charlotte Ids. to San Diego; 10-180m Guernea nordenskiodi (Hansen 1888) - N Atlantic to Prince William Sound, Alaska; 28-56m Lepechinella bierii J. L. Barnard 1957 – Tanner Basin to Cascadia Slope, Oregon 1000-1372m Lepechinella cura J. L. Barnard 1973 – Pacific Panama; 2234m Lepechinella echinata of Dickinson 1976 - Cascadia Abyssal Plain; 2800-3000m Lepechinella turpis J. L. Barnard 1967 – Baja Abyssal Plain; 1205-2706m Lepechinella uchu J. L. Barnard 1973 – Pacific Costa Rica; 3545-3563m

Lepechinella sp a of Dickinson 1976§ - Cascadia Abyssal Plain – 2800-3000m
Lepechinella sp b of Dickinson 1976§ - Cascadia Abyssal Plain - 2800-3000m
Nototropis atlassovi Gurjanova 1951 (=Atylus atlassovi)
Nototropis brüggeni Gurjanova 1938 (= Atylus brueggeni)
Nototropis tridens Alderman 1936 (=Atylus tridens)
*Paradexamine sp SD1 Pasko 1999§ - San Diego to San Francisco, generally in bays; 0-3m [introduced]
Polycheria carinata Bousfield and Kendall 1994 – British Columbia; 0m
Polycheria osborni Calman 1998 – SE Alaska to Galapagos Ids.; 0-15m
Prinassus nordenskioldi Hansen 1888 (=Guernea nordenskioldi)

<u>Family Dexaminidae</u> – Description: "Head free, not coalesced with peraeonite 1; exposed; as long as deep, or longer than deep, or deeper than long; anteroventral margin weakly recessed or moderately recessed or straight or concave, anteroventral margin deeply excavate or shallowly excavate, anteroventral corner rounded or hooked; rostrum present or absent, short or moderate or long; eyes present, well developed or obsolescent, or absent; not coalesced; 1 pair; not bulging. Body laterally compressed, or subcylindrical; cuticle smooth, or processiferous and dorsally carinate.

Antenna 1 shorter than antenna 2, or subequal to antenna 2, or longer than antenna 2; peduncle with sparse robust and slender setae; 3-articulate; peduncular article 1 shorter than article 2, or subequal to article 2, or longer than article 2; antenna 1 article 2 longer than article 3; peduncular articles 1-2 not geniculate; accessory flagellum present, or absent; antenna 1 callynophore absent. Antenna 2 present; short, or medium length, or long, or greater than body length; articles not folded in zigzag fashion; without hook-like process; flagellum shorter than peduncle, or longer than peduncle; less than 5-articulate, or 5 or more articulate; not clavate; *calceoli* absent.

Mouthparts well developed. *Mandible* incisor dentate; lacinia mobilis present on both sides; accessory setal row without distal tuft; molar present, medium, triturative; palp present or absent. *Maxilla 1* present; inner plate present, strongly setose along medial margin or weakly setose apically or without setae; palp present, not clavate, 1 - articulate or 2 -articulate. *Maxilla 2* inner plate present; outer plate present. *Maxilliped* inner and outer plates well developed or reduced, palps present, well developed or reduced; inner plates well developed, separate; outer plates present, very large or large or small; palp 4-articulate or 3-articulate, article 3 without rugosities. *Labium* smooth.

Peraeon. Peraeonites 1-7 separate; complete; sternal gills absent; pleurae absent.

Coxae 1-7 well developed, none fused with peraeonites. *Coxae 1-4* longer than broad or as long as broad or broader than long, overlapping or discontiguous, coxa 1 anteroventrally acuminate or coxae not acuminate. *Coxae 1-3* not successively smaller, none vestigial. *Coxae 2-4* none immensely broadened.

Gnathopod 1 not sexually dimorphic; smaller (or weaker) than gnathopod 2, or subequal to gnathopod 2; smaller than coxa 2, or subequal to coxa 2, or larger than coxa 2; gnathopod 1 merus and carpus not rotated; gnathopod 1 carpus/propodus not cantilevered; shorter than propodus, or subequal to propodus, or longer than propodus; gnathopod 1 slightly produced along posterior margin of propodus, or not produced along posterior margin of propodus, or not produced along posterior margin of sexually dimorphic;

subchelate, or parachelate, or chelate; coxa smaller than but not hidden by coxa 3, or subequal to but not hidden by coxa 3; ischium short; merus not fused along posterior margin of carpus or produced away from it; carpus/propodus not cantilevered, carpus short or elongate, shorter than propodus or subequal to propodus or longer than propodus, slightly produced along posterior margin of propodus or not produced along posterior margin of propodus.

Peraeopods heteropodous (3-4 directed posteriorly, 5-7 directed anteriorly) or 3-6 directed posteriorly, 7 directed anteriorly or homopodous (3-7 directed posteriorly), some or all prehensile or none prehensile. *Peraeopod 3* well developed. *Peraeopod 4* well developed. 3-4 not glandular; 3-7 without hooded dactyli, 3-7 propodi without distal spurs. Coxa well developed, longer than broad or broader than long; carpus shorter than propodus or subequal to propodus or longer than propodus, not produced; dactylus well developed. Coxa smaller than coxa 3 or subequal to coxa 3 or larger than coxa 3, acuminate ventrally or not acuminate, with well developed posteroventral lobe or without posteroventral lobe; carpus not produced. Peraeopods 5-7 with few robust or slender setae; dactyli without slender or robust setae. Peraeopod 5 well developed; shorter than peraeopod 6, or subequal in length to peraeopod 6, or longer than peraeopod 6; coxa smaller than coxa 4 or subequal to coxa 4 or larger than coxa 4, with posterodorsal lobe or without posterior lobe; basis expanded or linear, subrectangular, with posteroventral lobe or without posteroventral lobe; merus/carpus free; carpus weakly expanded, or linear; setae absent. Peraeopod 6 shorter than peraeopod 7, or subequal in length to peraeopod 7, or longer than peraeopod 7; merus/carpus free; dactylus without setae. Peraeopod 7 with 6-7 well developed articles; shorter than peraeopod 5, or subequal to peraeopod 5; similar in structure to peraeopod 6, or different in structure to peraeopod 6; with 7 articles; basis expanded or linear, without dense slender setae; dactylus without setae.

Pleon. Pleonites 1-3 without transverse dorsal serrations, pleonite 3 with dorsal carina or without dorsal carina; without slender or robust dorsal setae. *Epimera 1-3* present. *Epimeron 1* well developed. *Epimeron 2* setose, or without setae.

Urosome not dorsoventrally flattened; urosomites 1 to 3 coalesced, or 1 free, 2 and 3 coalesced; urosome urosomite 1 carinate, or urosomites not carinate, or urosomite 3 carinate; urosomites 1-2 without transverse dorsal serrations. Uropods 1-2 apices of rami with robust setae. Uropods 1-3 similar in structure and size. Uropod 1 peduncle without long plumose setae, without basofacial robust seta, without ventromedial spur. Uropod 2 well developed; without ventromedial spur, without dorsal flange; inner ramus subequal to outer ramus, or longer than outer ramus. Uropod 3 sexually dimorphic, or not sexually dimorphic; peduncle short or elongate; outer ramus longer than peduncle, 1articulate, without recurved spines. Telson laminar; deeply cleft; longer than broad; apical robust setae present, or absent." (Lowry and Springthorpe 2001).

Atylus - Only two of the eight species in this genus reported from the NEP range down to Central California or the SCB; *A. laevidensis* and *A. tridens*. Both are described in Bousfield and Kendall (1994), where they are separated by the first couplet in the key to the genus *Atylus*. Original descriptions are located in J. L. Barnard (1956), and Alderman (1936). The remaining species range from Arctic Alaska (*A. carinatus*, Shoemaker 1955), from the Northwest Pacific through Alaska (*A. atlassovi* and *A. brueggeni*, Bousfield and Kendall 1994), from the Northwest Pacific through Puget Sound (*A. collingi*, Bousfield and Kendall 1994), from Alaska to Puget Sound (*A. borealis*, Bousfield and Kendall 1994), or from British Columbia to Oregon (*A. georgianus*, Bousfield and Kendall 1994). It should be noted that the use of the form *bruggeni* by Bousfield and Kendall is incorrect. The animal was originally described as *Nototropis brüggeni* by Gurjanova (1938). Under the code prohibition of use of diacritical marks in species names this requires translitteration. The standard translitteration of an umlaut u is substitution of an e following the u. This renders the name translitteration as required by the code as *brueggeni*.

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Atylus nordlandicum from the North Atlantic (photo Cedric d'Udekem d'Acoz)

Guernea – Two species occur in the NEP, but only one is found in the SCB. G. nordenskioldi is circum-boreal, occurring in the North Atlantic, in the NW Pacific, and in the NEP as far south as Prince William Sound, Alaska. The local species G. reduncans was originally described in a new genus (*Dexamonica*) by J. L. Barnard (1958) which he later recognized as a synonym of Guernea (J. L. Barnard 1970). Despite continued description of species in the genus (J. L. Barnard 1972a,b; Hirayama 1985, 1986; Ishimaru 1987: Thomas and Barnard 1991) there does not appear to be a comprehensive key to the genus available. Separation of the two NEP species, both in the subgenus Prinassus (but see Ishimaru 1987 for arguments that the subgenus is invalid) is based on, among other things, the sharpness of the dorsal cusps on pereonites 6 and 7 and pleonites 1 and 2 in G. reduncans, and their obtuse bluntness in G. nordenskioldi. There are other differences in spination, etc., but in these small animals the larger characters of the dorsal ornamentation are more visible and useful. The two species do not, apparently, have overlapping distributions; with G. nordenskioldi not known south of the Gulf of Alaska, and G. reduncans not known north of British Columbia. SCB specimens will be G. reduncans.

Sexual dimorphism in *Guernea reduncans* is visible primarily in differences in the antenna 1 (much longer in females, with a very long slender flagellum), and in armature of the urosome. The dorsal cusp in males is retrorse, and narrows distally, while that of females is more rounded, compact, and not extended anteriorly. Females are also generally larger than males.

Lepechinella – other local dexaminoids come from shelf (*Guernea*, *Atylus*), or intertidal to shallow sublittoral depths (Atylus, Paradexamine, Polycheria), Lepechinella species are found from mid-bathyal to abyssal depths. There are several closely related "lepechinellid" genera (keyed in Bousfield and Kendall 1994, p. 32), but only species of Lepechinella are known from the NEP (Lepechinoides is known only from the North Atlantic [Thurston 1980], Lepechinopsis only from Madagascar [Ledoyer 1982], and Paralepechinella from the Indo-Pacific). Described species in the genus are nearly all treated in J. L. Barnard 1973, although a few additional species described later are listed in J. L. Barnard and Karaman (1991). Two of the NEP species are found in the SCB or adjacent to the south; L. bierii and L. turpis. Both are keyed in J. L. Barnard1973, as are L. uchu and L. cura, known from off Central America. Despite comments to the contrary in Bousfield and Kendall (1994), most of the remaining taxa are reported from the Cascadia Abyssal Plain or the adjacent bathyal slope off Oregon. Dickinsons record of L. echinata one would assume would have come from identification using Barnards key, which had become available several years prior. His erection of two provisional species in his 1976 thesis leaves us little to go on regarding their characteristics. He prepared no narrative description of these forms, and did not illustrate them. Attempts to locate the material for examination have not yet borne fruit.

Most records of the genus are based on one or a few individuals. The collections examined by Thurston (1980) however, allowed a view of both ontogenic change and sexual dimorphism in several species. As the patterns observed followed the same trend in all examined species, we can assume that they apply to lepechinellas from areas outside the North Atlantic as well. He found that, like other amphipods showing strong sexual dimorphism, the juvenile males and immatures resembled the females, and the males developed modifications to their morphology associated with sexual maturity. The general trends noted were basal thickening and increased deflexion of dorsal spines along the body with increasing age, and progressive enlargement of the urosomal dorsal cusp in males with age. Both the number and shape of cephalic spines appeared variable within a population, as did the degree of body setation. This later character was also considered to be of questionable value because such ornament was often quite brittle, and setae were frequently damaged or lost entirely due to handling in specimen preparation.

Paradexamine – a large genus in the tropics; few species reach as far into the temperate zone as the local provisional species *Paradexamine sp SD1*. The species is undoubtedly introduced, having shown up first in Catalina, apparently having arrived from warmer waters on a yacht. This first introduction was documented by Tony Chess of NMFS in 1991, who was working on small peracarids from algal turfs at the time. The species has since dispersed along the coast, and now occurs in shallow algal associated populations from San Diego to San Francisco. Its provenance remains obscure, as does its identity. J. L. Barnard (1972a, b) discusses this genus extensively, and provides (1972a) keys to the species known from the genus at the time. *Paradexamine sp SD1* does not conform to the key characters of any of the known species. A number of the original and subsequent descriptions of *Paradexamine* species remain to be obtained. Until comparison with full descriptions of all the possibly introduced species is completed, we must retain the local species as a provisional discrete from the named forms. Some reports of the species in evaluations of introduced species have been given the name *Paradexamine churinga*, a species described from Australia (J. L. Barnard

1972a). It is listed as *Paradexamine* sp. in Chapman (2007). The strong pleonal and urosomal armature of this species makes it stand out from other local dexaminoids.



Polycheria osborni (Drawing by Nancy Vander Velde)

Polycheria - Only one of the three NEP species occurs in California, *P. osborni*. The two other species are known only from British Columbia. The three taxa can be separated using the key provided by Bousfield and Kendall (1994). All materials so far examined from the SCB have been *P. osborni*. The ecology of this species is somewhat unusual. It lives in association with other invertebrates, where it constructs nests (i.e. Skogsberg and Vansell 1928; J. L. Barnard 1969; J. L. Barnard et al 1980; Bousfield and Kendall 1994). The classic association is with *Amaroucium* spp., firm compound tunicates found intertidally and subtidally on rocky reefs. The amphipod uses the prehensile dactyls of its pereopods to pull the test of the tunicate over it, forming a cavity within which it lays on its back and filter feeds. Personal experience in reef/cobble areas off San Onofre to 12m depths adds sponges to the list of potential hosts. In several encrusting species, *P. osborni* excavates into the sponge tissue, forming pits largely devoid of spicules in which the animal lays, extending its legs from a slit-like surface aperture to filter feed. This has not, to my knowledge, been reported in the literature, which deals only with tunicate hosts.

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