REDUCTION AND LOSS OF THE
PELVIC GIRDLE IN GASTEROSTEUS (PISCES):
A CASE OF PARALLEL EVOLUTION

By Michael A. Bell
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REDUCTION AND LOSS OF THE PELVIC GIRDLE IN
GASTEROSTEUS (PISCES): A CASE OF PARALLEL EVOLUTION

By Michael A. Bell

ABSTRACT: The structure of the pelvic girdle of Gasterosteus from a Recent population in Paxton Lake, Texada Island, British Columbia and a fossil assemblage from the Pliocene Truckee Formation, Hazen, Nevada is described. Ecological conditions inferred from the geology and paleontology of the Truckee Formation are consistent with the ecological requirements of living Gasterosteus. Based on paleoclimatological, ichthyofaunal and independent paleontological evidence, the fossil sticklebacks probably entered Nevada through the Death Valley region.

The structure of the pelvic girdle varied similarly in both samples from normally developed to entirely absent, with intermediate structures. In the fossil sample, specimens with normally developed pelvic girdles tended to be stratigraphically segregated from those with reduced pelvic structures. In both samples, specimens with developed pelvic girdles have more dorsal spines than those with reduced pelvic structures. The fossils lack lateral plates, but Recent specimens have 0 to 7, and specimens with developed pelvic girdles tend to have more than those with reduced structures. Other correlations with pelvic structure were found.

While there is a suite of correlated characters common to both samples, details of their variation differ. Differences between the two samples include the shape of pelvic vestiges, the arrangement of dorsal spines on predorsal radials, presence of lateral plates, the number of dorsal spines and the range of some other meristic characters. Based primarily on zoogeographic considerations, the two samples are believed to represent independent phyletic lines. Morphological similarity is due to parallelism and not convergence.

Variation in pelvic structure and other characters correlated with pelvic structure do not indicate that either the Recent or fossil sample is composed of more than one species. Gasterosteus apodus Mural (1973) is regarded as a junior synonym of Gasterosteus doryssus (Jordan, 1907). Gasterosteus doryssus should be maintained until the status of living populations of Gasterosteus with reduced pelvic structures can be evaluated according to the biological species concept.

Reduction of the pelvic girdle and dorsal spines similar to that reported for Gasterosteus in this study have been reported previously for two other gasterosteid genera, Pungitius and

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Culaea. There has been parallelism within and between these three genera. Although evidence concerning the selective mechanism is not presented in this paper, considerable evidence exists that predator selection of those structures reduced in these genera is very important.

Selection is probably responsible for the production of parallel phenotypes in widely dispersed samples of Gasterosteus and is probably the most important factor in its geographic variation. This phenomenon is very common among all organisms. Similar parallelisms within three gasterosteid genera lend support to Vavilov's theory of homologous series in variation. Ubiquitous parallelism poses a serious problem for systematists and zoogeographers working at the species level.

INTRODUCTION

Parallelism is a common feature among many groups of organisms. This phenomenon is generally believed to be a consequence of adaptation to similar environments. Within the sticklebacks (Gasterosteidae) parallelism is probably responsible for an unusual distribution pattern of phenotypes of species in at least three genera. Gasterosteus, Pungitius, and Culaea populations are occasionally found which tend to lose or reduce the normally strong pelvic girdle. Variable presence or absence of the pelvic girdle in sticklebacks was first reported by Day (1878) who described it in the threespine stickleback, Pungitius pungitius (Linnaeus), from Ireland. Nelson (1971a) has since described populations of P. pungitius from Ireland and Canada, and Coad (1973) reported additional populations from Canada, in which the pelvic girdle may be normally developed, reduced to a vestigial plate or absent. Such variation was also reported by Nelson (1969) and Nelson and Atton (1971) in Canadian populations of the brook stickleback, Culaea inconstans (Kirtland). Penczak (1965) described pelvic girdles of White Sea Gasterosteus aculeatus Linnaeus in which the ascending branch of the pelvic girdle is short. Gasterosteus populations in which the pelvic girdle may be reduced or absent have been mentioned (Hagen and McPhail, 1970; Nelson, 1971a, 1971b; Nelson and Atton, 1971) and Moodie and Reimchen (1973) have discussed such a population from the Queen Charlotte Islands, British Columbia. However, pelvic variation in populations of Gasterosteus in which the pelvic girdle tends to be reduced has not been described in detail.

The fossil stickleback, Gasterosteus doryssus was originally described as Merriamella doryssa by Jordan (1907) who considered it to be an atherinid (silversides). He was misled by the absence of the characteristic Gasterosteus pelvic girdle and spine from his specimens. One month later, Hay (1907) described other fossils of the same species as Gasterosteus williamsoni leptosomus based on specimens from the same locality as Jordan's type. One of Hay's specimens had a normal pelvic girdle but in the others, it was incompletely developed. Although Hay described the variation in pelvic structure in his small sample, he did not comment on its significance. Jordan (1908)
made no mention of the pelvic girdle and he attributed differences between his material and Hay’s to incomplete preservation. Mural (1973) interpreted these differences in pelvic structure to indicate the presence of two species, *G. doryssus* with normal pelvic structure and a new species, *Gasterosteus apodus*, with vestigial or no pelvic structures.

I have examined the pelvic girdles in a large series of fossils of the nominal species *G. doryssus* and *G. apoda* and found that differences in the pelvic structure between Jordan’s and Hay’s specimens represent morphological variation and not the state of preservation of the fossils. I have also examined a sample from a population of similar sticklebacks from Paxton Lake, Texada Island, British Columbia. The purpose of this study is to describe variation in the structure of the pelvic girdle in these samples and the relationship of pelvic structure to other morphological features.

**Materials and Methods**

Fossil *Gasterosteus doryssus* in the collections of the following institutions have been examined: Natural History Museum of Los Angeles County, Section of Vertebrate Paleontology (LACM); California Academy of Sciences, Department of Geology (CAS); and University of California, Berkeley, Museum of Paleontology (UCMP). Several unnumbered specimens were received from C. A. Repenning of the U. S. Geological Survey, Menlo Park, California.

Specimens of *G. doryssus* come from near Hazen, Lyon County, Nevada. LACM Material is from LACM vertebrate paleontology locality LAV 6663 (==UCMPV 66146). This locality is in secs. 9 and 10, T. 19 N, R. 25 E (approximately N 39°32’, W 119°10’), Two Tips Quadrangle, Nevada. The CAS specimens are also from this locality. The locality is a commercial diatomite quarry situated on the northeast slope of the Virginia Range and is reached by dirt road beginning at the east end of the Fernley Farm District Road and winding southward. The matrix at this locality and others in the Middle Truckee Formation is a very pure, finely laminated diatomite with occasional laminae of sand and tuff. The dip of the beds seems generally to conform to the surface topography. The UCMP specimens come from localities UCMPV 1034, 5613, and 6998. Repenning’s specimens were collected in sec. 17, T. 19 N, R. 26 E, at a distance of about 8 km from LAV 6663.

Fossil specimens examined were LACM 17439 to 17475, 17924 to 17945, and 28090 to 28126; CAS 50033 to 50054 from locality LAV 6663 UCMP 9372 (type of *Merriamella doryssa*), 9374 and 9375 from locality UCMPV 1034; UCMP 58565 from locality UCMPV 5613; and Repenning’s unnumbered specimens. All of these specimens are skeletons preserved on slabs of laminated diatomite of the Middle Member of the Truckee Formation. UCMP 99674 from locality UCMPV 6998 (Brady Pocket, MacDonald, 1956) consists of isolated elements from the Lower Member of the Truckee Formation.
The fossil fish were found by splitting the laminated diatomite along the bedding planes with a knife. This procedure usually split the fish skeletons and sometimes individual bones down their centers so that portions of the skeleton were represented on both slabs resulting from the cleavage of the rock. Thus, preparation to improve the quality of the specimens was impractical. Specimens discovered by this method were collected or discarded depending on their state of preservation and the abundance of their morphological type among previously collected specimens. Specimens with well developed pelvic structures or more than one dorsal spine were usually retained regardless of condition, but specimens with vestigial pelvic girdles or fewer than 2 dorsal spines may have been discarded. Thus, the frequency of pelvic structures or individuals with different numbers of dorsal spines is not considered per se without taking this bias into account. Specimens LACM 28090 to 28126 form a series of specimens in which all fossils were retained. With the exception of this collection, the fossils studied in this report do not represent a random sample of those fossils available in the deposit. Some specimens were partially or entirely covered with matrix after splitting and were prepared further by removing the matrix with needles. The fish fossils were sprayed with acrylic aerosol following preparation to harden their surfaces.

Specimens of Recent *Gasterosteus* from a population in which the pelvic girdle may be normal or reduced were supplied by J. D. McPhail and D. Hay of the Institute of Animal Resource Ecology, University of British Columbia. This collection is from Paxton Lake, Texada Island, British Columbia. The lake is occupied by two populations of *Gasterosteus*, one benthic and the other pelagic. The sample I studied is the benthic form (D. Hay, pers. comm.). Texada Island was subjected to postglacial marine submergence, so the habitat is probably less than 5,000 years old (J. D. McPhail, pers. comm.). The sample I received has been deposited in the Ichthyology collection of the LACM and catalogued LACM 32008-1 (202 specimens).

Recent specimens of *Gasterosteus aculeatus* from southern and central California were examined to determine the frequency of individuals with different number of dorsal spines. The following specimens from the Ichthyology collection of the LACM were examined (number in parentheses are the number of specimens examined): LACM 30899-1 (316), Alamo Creek, Santa Barbara County; 30922-1 (310), Twitchell Reservoir, San Luis Obispo County; 30943-1 (60), Santa Clara River, Los Angeles County; 30946-1 (341), Ventura River, Ventura County; 31420-1 (103), Los Berros Creek, San Luis Obispo County; 31421-2 (79), Arroyo Grande Creek, San Luis Obispo County; 31422-1 (177), San Antonio Creek, Santa Barbara County; 31423-1 (350), Santa Ynez River, Santa Barbara County; 31424-2 (305), Salsipuedes Creek, San Luis Obispo County; and W71-10 (148), Big Pico Creek, San Luis Obispo County.

All specimens in LACM 32008-1 were stained with alizarin to allow inspection of bony elements near the body surface. Sixty-seven specimens
were selected for pelvic structure and cleared and stained using the Taylor (1967) technique.

Standard measurements (outlined below) were made on the cleared and stained specimens in LACM 32008-1 and 115 fossil specimens LACM 17439 to 17475, 17924 to 17945, 28090 to 28126, and CAS 50033 to 50054. The pelvic condition and number of lateral plates and dorsal spines were determined in all specimens in LACM 32008-1.

The standard measurements were devised to compare the fossil assemblage with the Recent population, to determine whether correlations between pelvic structure and other structures exist, and to measure as many structures as possible which could be seen on most of the fossils. The measurements were made following the procedures of Hubbs and Lagler (1964) except as noted below:

2. Total number of vertebrae.
3. Predorsal radials; the number of proximal radials (but possibly including predorsal bones of Smith and Bailey, 1961) anterior to and including the radial normally bearing the last dorsal spine in Gasterosteus aculeatus (see Lindsey, 1962, Fig. 1).
4. Number or dorsal spines.
5. Number of dorsal fin rays; the last two rays were counted separately.
6. Number of anal fin rays; the last two rays were counted separately.
7. Number of lateral plates; all plates were counted on both sides regardless of plate size. All specimens counted were greater than 25 mm SL, the length at which all plates have appeared (Hagen and McPhail, 1970).
8. Length of dorsal spines; measured from the top of the proximal radial to the tip of the spine with an ocular micrometer.
9. Pelvic girdle structure; classified as developed, vestigial or absent.
10. Predorsal radial and spine arrangement; the notation of Penczak (1960) in which the radial or predorsal element is represented by a Roman numeral and the position of the dorsal spines by Arabic numeral superscripts on the appropriate Roman numeral was used.

The data obtained from the standard measurements were grouped according to pelvic morph and the grouped data were plotted in histograms (Fig. 5) or their means were calculated (Table 1). The distributions shown in Fig. 5 were examined using the Kolmogorov-Smirnov Test (Tate and Clelland, 1959) to determine if there were statistically significant differences at the 0.05 confidence level in the distribution of character states between pelvic classes. The distribution of ranked dorsal spine lengths were also examined in this manner.

Skeletal elements were drawn using a camera lucida attachment on a
dissecting microscope. Figures were photographed by L. S. Reynolds, staff photographer of the LACM.

**Stratigraphy**

The Truckee Formation was originally described by King (1878). The original description contained misleading and incorrect information according to Axelrod (1956) who redrew the type section. Axelrod recognized three members in the formation totaling about 760 m (2500 ft), but Ruben (1971) indicated that the Truckee Formation is 1021 m (3350 ft) thick. The Lower Member of the Truckee Formation is composed of basalt tuff overlain by sedimentary breccia primarily composed of reworked basalt tuff. This is overlain by limestone rich in mollusks, followed by blue-grey sandstone, thin diatomite and basalt tuff. This member of the formation totals 43 to 49 m (140 to 160 ft) thick. The middle member is primarily nearly pure diatomite generally occurring in beds up to 0.3 m thick but much thicker in the quarries. Pumice beds scattered throughout the section range from a few centimeters to about a meter thick and there are local 8 to 10 cm thick blue-grey sandstones. The Middle Member of the formation is about 460 m (1500 ft) thick. The upper member is characteristically slabby grey limestone ranging from a few centimeters to 9 m (30 ft) thick. The limestones are regularly interbedded with grey sandstones, paper-thin lenses of diatomite, and black and red basalt pebble conglomerates. This member is at least 260 m (850 ft) thick, but Axelrod did not see the top of the formation.

Axelrod (1956) mapped the Truckee Formation in the area northeast of Brady's Hot Springs, Churchill County, about 35 km (23 miles) northeast of locality LAV 6663 near Hazen. His map shows outcrops of the middle member of the formation scattered over an area of about 16 sq. km. Middle Truckee rocks abruptly disappear due to faulting to the southeast and they are overlain by younger sediments and alluvium to the west, north and east. The beds generally dip to the northwest at 12 to 35° except at the southern extremity of the outcrops where they dip to the southeast at the edge of a fault. The area of deposition of Middle Truckee sediments in the Brady Hot Springs region must have been greater than that exposed, but the area of the lake in which deposition took place was not necessarily as large at any time as the basin in which the Truckee Formation was deposited. The lake may have occupied and deposited sediments in different portions of the basin at different times. Rubin (1971) has suggested that the Truckee Basin contained several interconnected lakes in the Pliocene. Confusion of the names applied to Tertiary formations in west-central Nevada makes difficult more precise statement of the aerial extent of Middle Truckee rocks or the size of the lake inhabited by *Gasterosteus*.

**Age of Fossil Deposits**

With the exception of UCMPV 6998, which is in the Lower Member of the formation, all localities for fossil *Gasterosteus* are in the Middle Member
of the Truckee Formation as defined by Axelrod (1956). Ruben (1971) reviewed the age of the Truckee Formation indicating that it extends from Early to Middle Pliocene, basing his interpretation on correlations of Stirton (1939). The presence of numerous fossil fish (Stirton, 1939) indicates that Stirton's fossils were from the Middle Member of the Truckee Formation. Buwalda (1914) had reported a proboscidean tooth from the Truckee Formation considered to indicate an age no greater than Middle Miocene. MacDonald (1950 and 1956) reported fossil mammals from the Lower Member of the Truckee Formation that indicate an Early Pliocene age.

Age determinations of specimens of *G. doryssus* have been rather confused. Following Merriam's advice, Jordan (1907) stated that his material was probably Miocene. Hay (1907) mistakenly believed that the sticklebacks he studied came from the Pleistocene Lahontan Beds. This error was perpetuated, notably by Jordan (1908) and Hubbs and Miller (1948), until it was corrected by La Rivers (1953) who recognized that the fossil sticklebacks came from the Pliocene Truckee Formation. Axelrod's (1948 and pers. comm.) "Hazen flora" which is Middle Pliocene, came from the type locality of *G. doryssus* (UCMPV 1034). On the basis of information supplied by Axelrod, Miller (1955) concluded that specimens of *Fundulus nevadensis* (Eastman, 1917) which occur with *G. doryssus* were of Early Pliocene age. Uyeno and Miller (1963) accepted this conclusion. Axelrod (pers. comm.) has also tentatively suggested an age of Early Pliocene for locality LAV 6663 based on a few plant remains which I sent to him.

Yen (1950) believed that mollusks from the type section of the Lower Member of the Truckee Formation represent a Pliocene assemblage even though a Miocene species is present. (Yen did not give the stratigraphic position within the Truckee Formation of his collections, but Axelrod (1956) stated that they came from the lower member of the formation.) On the basis of a characteristic Miocene diatom (*Melosira granulata*) identified by G. D. Hanna, M. Ghiiorso (pers. comm.) considers locality LAV 6663 to be Late Miocene.

Correlations to determine the age of assemblages of *G. doryssus* based on mammalian, higher plant, diatom, and mollusk fossils tend to produce conflicting results. This inconsistency may be due to the deposition of *G. doryssus* and the Middle Member of the Truckee Formation over a long period of time. Perhaps the earliest record of *G. doryssus* is from the Late Miocene. It persisted through the Early Pliocene to the Middle Pliocene at which time it was deposited with the Hazen flora. Based on Axelrod's (1948, 1957, 1958) estimates that the deposits are Clarendonian to Hemphillian and the conclusions of Everden, et al. (1964), the deposits in which *G. doryssus* occurs are probably at least 10 million years old.

**Paleoecology**

Axelrod (pers. comm.) has inferred from fossil plants at locality LAV
6663 and his Hazen flora (Axelrod, 1948) some of the climatic conditions in which *G. doryssus* lived. There was an equable climate with warm but rarely hot summers and mild winters. There may have been occasional light frosts. Average yearly rainfall was at least 38 to 44 cm (15 to 18 inches) but may have been greater. Summer rainfall is also indicated.

Yen (1950) made paleoecological inferences based on mollusk assemblages which came from the Lower Member of the Truckee Formation. He believed that the diversity of the assemblages which came from the Lower Member of the Truckee Formation indicates deposition in a large body of water. The considerable distance between localities for *G. doryssus* (about 8 km) and between the type section of the Truckee Formation and fossil localities also tends to support this view. There were muddy and stony shores. Variation in size, sculpture, and height of the shells possibly indicates a variety of water velocities and pH. Abundant rissoid and planorboid snails indicate a habitat rich in aquatic filamentous algae and leafy plants. Freshwater limpets, which feed on algae and diatoms and prefer rocky bottoms with still water, are also present.

It is, of course, difficult to evaluate the relevance of Yen's inference to the paleoecology of the middle member of the formation. By Middle Truckee times, water condition may have changed and much sedimentation had occurred. Ruben (1971) discussed Middle Truckee paleoecology. He believed that the diatomites were deposited in quiet water near shore. The lake water was slightly saline and part of a larger basin and range system. Ruben suggested that the presence of encysted diatoms indicates extreme seasonal dry conditions, but this suggestion is inconsistent with Axelrod’s inferences on climatic conditions and encystment could have resulted from other adverse conditions.

Living *G. aculeatus* inhabit very diverse habitats. This species is found in waters of varying salinity, temperature, color, depth and velocity, over substrates of varying particle size and vegetation type. None of the inferences on the paleoecology of the Middle Member of the Truckee Formation is inconsistent with these broad ecological tolerances. It is interesting that the only fish genera known from the Truckee Formation, *Gasterosteus* and *Fundulus*, have distributions centered in coastal marine and brackish water and low gradient coastal streams. Seasonal drying resulting in elevated salinity suggested by Ruben (1971), may account for the presence of only these two euryhaline fishes.

There is evidence that *G. doryssus* was subject to predation. One snake reported to be a *Coluber* has been described with *G. doryssus* as stomach contents (Ruben, 1971). Coprolites produced by animals apparently large enough to eat *Gasterosteus* are common in Middle Truckee beds, although they contain no stickleback bones. Bell (1973a) has reported coprolites from the Pleistocene Bautista Formation containing recognizable stickleback spines. Their absence from coprolites in the Truckee Formation may indicate that
sticklebacks were not the prey. A cormorant in the LACM vertebrate paleo-
ontology collection (H. Howard, pers. comm.) has been collected from Mid-
dle Truckee rocks and cormorants feed exclusively on fishes. However, there
is no evidence that the fossil specimen preyed on sticklebacks. No piscivorous
fishes (Uyeno and Miller, 1963) or other potential predators on G. doryssus
have been reported from the Truckee Formation. Hagen and Gilbertson
(1972) found that Gasterosteus that are preyed upon by other species of
fishes tend to have longer fin spines and a modal number of seven lateral
plates. Thus, one would not expect from the morphology of G. doryssus
(plate-less, pelvic-less, and reduced dorsal spines) that it was preyed upon
by other species of fishes.

ZOOGEOGRAPHY OF FOSSIL GASTEROSTEUS

Neither the phylogenetic relationships nor the geographic origins of the
Gasterosteidae are well understood. Sticklebacks do not appear in the fossil
record until the Early Pliocene or possibly very late in the Miocene. Only the
modern genera Gasterosteus (Bell, 1973a) and Pungitius (Schtyleco, 1934;
Berg, 1965) are known as fossils. Pungitius haynesi David (1945) is a Gas-
terosteus (Bell, 1973b). The five gasterosteid genera are very distinct and
their interrelationships are poorly understood (Nelson, 1971b). Although the
family is composed of widespread amphiboreal species, its distribution seems
to be centered in the North Atlantic. According to Durham (1950) and
Axelrod and Bailey (1969), there has been progressive cooling throughout
the Tertiary with only minor fluctuations. Wolfe (1971) has suggested more
dramatic Tertiary climatic fluctuations, but these were not of sufficient magni-
tude to allow Gasterosteus to enter the Pacific Ocean by dispersing along the
southern coast of North America. Regardless of where Gasterosteus arose,
it must have entered the Pacific ocean from the north through the Bering
Straits area.

Modern Gasterosteus are peripheral freshwater fish (Darlington, 1957).
Such fishes belong to groups restricted to freshwater adjacent to the sea or
so recently derived from marine ancestors that their present distribution is
the result of dispersal through the sea. The distribution and physiology of
living Gasterosteus aculeatus conforms to this definition (Münzing, 1963).
Thus, there have been two potential routes for southward movement of the
ancestors of G. doryssus: along the coast in marine water as trachurus popula-
tions or over land in fresh water as leiurus populations. The names trachurus
and leiurus have been applied to modal anadromous and freshwater Gas-
terosteus phenotypes respectively. The taxonomic status of these names is
presently a point of contention (Hagen and McPhail, 1970; Miller and
Hubbs, 1969).

Based on the present range of the completely plated, anadromous form
of G. aculeatus (Miller and Hubbs, 1969), the trachurus type, breeding
populations seem to be restricted in California to waters where the mean
Figure 1. Map of the possible invasion routes (stippled), 1, the northern and 2, the southern, by which the ancestors of Gasterosteus doryssus could have entered Nevada. The heavy line represents the shore line in the Late Miocene and the light line the present coast. The latitude in the Miocene of the minimum water temperature inhabited by extant marine (trachurus) breeding populations of Gasterosteus aculeatus in California is indicated by the horizontal arrow.
February surface temperature exceeds 12.4°C. This isotherm would have intersected the shoreline at about 43°N (Fig. 1) in the Late Miocene according to Durham's (1950) Fig. 3. However, even short term temperature declines would have allowed Gasterosteus to move a great distance southward along the coast. Hubbs (1948) reported northward range extensions of tropical fishes of hundreds of miles in the 1850's. The presence of the salmonid, Smilodonichthys rastrosus Cavender and Miller (1972) in the Early Pliocene, marine Capistrano Formation in Orange County, California (L. Barnes, pers. comm.) indicates that marine waters had cooled sufficiently to allow cold water fish species to move into southern California. Thus, it is not surprising that Gasterosteus has been reported from the Pliocene Ridge Formation in Los Angeles County (David, 1945; Bell, 1973b). Gasterosteus had reached at least as far south as Los Angeles County by the Pliocene and could have entered fresh water anywhere north of this point to reach the site of deposition at Hazen, Nevada (about 39°N). The establishment of partially plated, freshwater or leirurus type populations from trachurus populations could have easily taken place because leirurus populations have been established repeatedly from marine stocks (Hagen, 1967; McPhail and Lindsey, 1970; Münzing, 1959, 1963).

The terrain across which the freshwater ancestors of G. doryssus dispersed was very different from that of western North America today. At the end of the Miocene, the present position of the Sierra Nevada was occupied by a broad ridge with the summit at about 900 m (about 3000 feet) elevation, gradually increasing to about 1500 m (about 5000 feet) in the south and decreasing to about 300 m (about 1000 feet) to the north (Axelrod, 1957 and 1962a). Three to 6 km (about 2 to 4 miles) wide valleys crossed the Sierran ridge north of Yosemite (Axelrod, pers. comm.) at elevations of 600 to 750 m (about 2000 to 2500 feet) (Axelrod, 1957). These valleys contained rivers with their headwaters in western Nevada at an average elevation of about 600 to 750 m (Axelrod, 1957 and 1962b). Axelrod (1958) noted that the Truckee Formation includes sediments carried eastward from the region of the Sierra, but this fact does not preclude drainage of the basin to the Pacific Coast. The rivers north of Yosemite are one possible route (route 1, Fig. 1) by which Gasterosteus may have invaded Nevada.

There is considerable zoogeographical and paleontological evidence for a more southerly route (route 2, Fig. 1) of invasion. Miller (1958) reviewed the similarities of the fish faunas of the Lahontan Basin (within which the Truckee Formation is located) to other basins and found similarities to the Death Valley, Klamath, Columbia, and Bonneville River systems. Miller (1958) believed that the connection between the Lahontan Basin and the latter three river systems existed no earlier than the Middle Pliocene. He suggested that fossil sticklebacks reached the Lahontan Basin through the Death Valley region in Late Miocene or Early Pliocene times. Hubbs and Miller (1948) pointed out that most of the 8 fish species endemic to the Lahontan
Basin are lowland forms not capable of crossing an elevated divide. This would necessitate access to the Lahontan Basin through the area south of the Sierran ridge. Miller (1946) gave evidence which supports this view. Siphatales is known as either a Recent or fossil occupant of both the Death Valley and Lahontan Basins. The presence of Empetrichthys in Pahrump Valley also supports his view. The Owens River stock of Catostomus is most closely related to and probably derived from C. tahoensis of the Lahontan Basin. In 1958, Miller added evidence for the Tertiary connection between the Death Valley and Lahontan Basins. The fossil killifishes, Fundulus curryi and Fundulus eulepis, similar to Fundulus nevadensis of the Truckee Formation, occur in Late Tertiary deposits of Death Valley (Miller, 1945). Pantosteus santaeannae, which probably reached the Pacific coast in the Pliocene, is most closely related to Great Basin forms. Thus, there is considerable faunal evidence to indicate a Late Tertiary connection between the Death Valley and Lahontan Basins through which Gasterosteus could have dispersed.

RESULTS OF MORPHOLOGICAL STUDIES

Pelvic Variation

Variation in the pelvic structure is very similar in the Recent and fossil collections of Gasterosteus, ranging from normal development to entire absence. However, it is useful to recognize 3 pelvic classes. The different classes in the Recent and fossil materials can be discussed together.

Developed: Twenty-four fossil specimens ranging from 34.0 to 73.3 mm SL and 23 Recent specimens ranging from 34.1 to 57.2 mm SL were examined. The developed pelvic girdles of the Recent sample and the fossils conform to the description by Nelson (1971b) except that the anterior margin of the pelvic girdle is incised, forming a strong anterior process (Fig. 2a; 3a, b, c). In the Recent specimens, the pelvic spines are denticulated. The ascending branch of the pelvic girdle may be forked or unforked but is usually fairly bilaterally symmetrical. When forked, a lateral plate generally lies between the forks. In the fossils, the ascending branch of the pelvic girdle is not forked to accommodate a lateral plate because lateral plates are lacking. The pelvic spine of the fossils, unlike that of most Gasterosteus, is undenticulated (the dorsal spines are also undenticulated). However, Gasterosteus has been reported with undenticated spines previously (Penczak, 1962a, 1964). Gasterosteus fin spines from the Lower Member of the Truckee Formation (locality UCMP 6998) are denticulated. Pelvic spines are recognizable by enlarged denticles along the ventral margin.

Vestigial: Sixty-seven fossil specimens ranging in size from 24.4 to 68.1 mm SL and 25 Recent specimens ranging from 33.7 to 63.2 mm SL were examined. Only one vestige is found in 21 of the fossil and 4 of the Recent specimens examined. Pronounced bilateral asymmetry is common (Fig. 2c, d, e, h; 4b, e), especially in the Recent sample. The fossil and Recent materials differ
Figure 2. Camera lucida drawings of pelvic girdles (with the ectocoracoid above for orientation) of Recent Gasterosteus (LACM 32008-1): a is normally developed and b through h is a series of vestiges in order of decreasing development. The pelvic spine denticles are not shown.
Figure 3. Reconstructions from camera lucida drawings of normally developed pelvic girdles of *Gasterosteus doryssus*: a, LACM 17442; b, 17452A; and c, 17452B. The pelvic girdle was flattened during preservation so that its ventral and lateral surfaces shown here lie in the same plane. The pelvic spines are not shown. Broken lines are estimates of the bone margins covered by other elements or which have been broken and are represented by impressions in the matrix.

Figure 4. Reconstructions from camera lucida drawings of pelvic vestiges of *Gasterosteus doryssus* in order of decreasing development: a, LACM 17452C; b, 17944A; c, 17940A; d, 17941A; e, 17461; f, 17463; g, 17944B; and h, 17474A. Broken lines are estimates of the bone margins covered by other elements or which have been broken and are represented by impressions in the matrix.
in that the tear-drop shaped vestige shown in Fig. 4d to f is very common in the fossils. In the fossils, very small vestiges tend to be irregularly shaped (Fig. 4g, h). There are also some rather large vestiges which have shapes intermediate between those of the developed and vestigial classes (Fig. 4a, b). The pelvic girdle of CAS 50046 is much reduced in size but resembles the normal pelvic girdle, complete with spines. In LACM 17944A (Fig. 4b), one of the pelvic vestiges is the typical tear-drop shape and the other has the form of the developed pelvic bone but is smaller, flat, and lacks the spine. Jordan's (1907) type of *Merriamella doryssa* (UCMP 9372) and other specimens labeled as type, cotype or paratype (UCMP 9374 and 9375), all from the type locality (UCMPV 1034), and UCMP 58565 (from locality UCMPV 5613) have intermediate shaped pelvic vestiges. Pelvic vestiges of Recent specimens are relatively variable in shape (Fig. 2b to h), but smaller vestiges tend to be roughly tear-drop shaped. Nine of the 25 specimens with pelvic vestiges have a reduced spine on one or both vestiges. Such spines are denticated.

*Absent:* No sign of the pelvic girdle is found in 24 of the fossil specimens ranging in size from 24.2 to 64.4 mm SL and 19 Recent specimens ranging from 33.1 to 63.1 mm SL. It is possible that some of the smaller specimens had unossified pelvic vestiges which would have ossified if they were older, because the pelvic girdle develops relatively late in ontogeny (Nelson and Atton, 1971; Swarup, 1958). However, many of the specimens are large. It is also possible that pelvic vestiges in the fossils could have been lost prior to burial, but all of these specimens are otherwise well preserved, and there is no reason to believe that the pelvic vestiges were selectively lost when all other structures are in place.

**Stratigraphic Distribution of Fossil Classes**

The distribution of the pelvic classes through time is difficult to determine from available data. Fossil sticklebacks occur from at least Early Pliocene to Middle Pliocene. Most of the material available for this study was collected from Early Pliocene portions of the Middle Member of the Truckee Formation. Unfortunately, most of the fossils were collected from loose rubble or are without field data. Thus, their relative stratigraphic positions cannot be determined.

UCMP 99674 from the Lower Member of the Truckee Formation includes isolated pelvic spines which are well denticulated. At least some Lower Truckee sticklebacks had normally developed pelvic girdles.

LACM 28090 to 28126 were collected *in situ*. These specimens have a vestigial pelvic girdle or no girdle. None has a developed pelvic girdle. One of the specimens collected *in situ* has two dorsal spines, and the remainder have one.

Another source of information is slabs with two or more specimens. LACM 17452 includes 3 specimens, 2 of which have developed pelvic girdles (Fig. 3b,
c) and the third of which has a girdle intermediate between the developed and vestigial classes (Fig. 4a). On LACM 17452, the specimens with developed pelvic girdles have 1 and 3 dorsal spines, and the specimen with the intermediate girdle has 2. CAS 50044 has 2 specimens with developed pelvic girdles, but the dorsal spines could not be counted. LACM 17944 has 4 specimens, 1 of which has 1 vestigial pelvic element and 1 intermediate between developed and vestigial (Fig. 4b) whereas the remainder all have typical pelvic vestiges. One of the latter specimens lacks dorsal spines, and the remainder have 1. LACM 17440 (2 specimens), 17469 (2 specimens), 17474 (2 specimens), 17937 (2 specimens), 17940 (2 specimens), and 17942 (8 specimens) have only fish with vestigial pelvic girdles. All but 2 of these slabs (LACM 17474 and 17940) have fish with differing numbers of dorsal spines (either 0 and 1 or 1 and 2) and LACM 17942 has fish with 0 to 2 dorsal spines. Two slabs, LACM 17941 (3 specimens) and LACM 17943 (4 specimens) have fish with either vestigial or no pelvic girdles. All of these specimens have one dorsal spine. No slabs were found on which all fish lack the pelvic girdle.

Analysis of the stratigraphic distribution of fossil sticklebacks has limitations. Specimens occurring on one slab or which were collected in situ within a restricted section of the formation generally do not come from precisely the same layer of diatomite and must have been deposited at different times. Even if two specimens occur on precisely the same layer, they were not necessarily sympatric. They may have come to rest in the same area following death. Conversely, incomplete sampling may result in the erroneous impression that two classes are isolated from each other stratigraphically.

The effect of such limitations on this analysis is minimal because the sample size is fairly large, and different classes of sticklebacks seem to be segregated, eliminating the first two limitations. Thus, the distribution pattern is relatively easy to interpret. Fish with the developed pelvic girdle tend to be segregated from those in which the pelvic girdle is reduced. The only exception to this general pattern is LACM 17452 as noted above. Sticklebacks with vestigial and no pelvic girdle occur together as fossils but may not have been sympatric. The apparent segregation of the developed class from other classes may be the result of geographic or temporal separation.

The earliest known sticklebacks from the Truckee Formation are from the Lower Member. Some of these had normal pelvic girdles with denticulated spines. From my series it is impossible to determine if sticklebacks with vestigial pelvic girdles occur in the Lower Member of the formation. Locality LAV 6663, where all three pelvic morphs occur, penetrated only a restricted portion of the Middle Member of the Truckee Formation so all pelvic morphs occur in the Early Pliocene part of the Middle Member of the Truckee Formation. Jordan's (1907) and Hay's (1907) Middle Pliocene type material had varying pelvic structures. There are two possible explanations for this distribution pattern. These specimens may have come from polymorphic populations with varying proportions of the pelvic classes, or there may have been two
biological species of *Gasterosteus*. If there were polymorphic populations, they would probably have consisted primarily of individuals with developed pelvic girdles or primarily of the vestigial and absent classes. This polymorphism must have persisted from Early to Middle Pliocene. Fish with different numbers of dorsal spines were probably less segregated from each other than were those with developed pelvic girdles from ones with vestigial and no pelvic girdles.

*Characters Correlated With Pelvic Structure*

The number of dorsal spines, dorsal fin rays, predorsal radials, anal fin rays, total vertebrae and the length of the last two dorsal spines expressed as a percent of standard length (SL) were examined in the fossil and Recent material to determine whether any were correlated with pelvic structure. The number of lateral plates was also compared between the different pelvic classes in the Recent sample. Means of the spine lengths were calculated using only individuals of 40 to 60 mm SL to minimize the effect of allometric growth, known to take place throughout life in *G. aculeatus* (Bertin, 1925; Hagen and Gilbertson, 1972). Mean spine lengths are shown in Table 1. The distributions of character states within the range of variation of meristic characters for the

Table 1. Mean spine lengths of the different pelvic classes: DEV, developed; VEST, vestigial and ABS, absent. Numbers in parentheses are sample sizes.

<table>
<thead>
<tr>
<th>Fossil</th>
<th>DEV</th>
<th>VEST</th>
<th>ABS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Second dorsal spine</td>
<td>8.37 (9)</td>
<td>6.60 (5)</td>
<td>2.38 (1)</td>
</tr>
<tr>
<td>Third dorsal spine</td>
<td>3.90 (9)</td>
<td>2.96 (30)</td>
<td>2.56 (10)</td>
</tr>
<tr>
<td>Recent</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Second Dorsal spine</td>
<td>6.97 (18)</td>
<td>6.66 (20)</td>
<td>6.50 (13)</td>
</tr>
<tr>
<td>Third dorsal spine</td>
<td>2.26 (18)</td>
<td>2.17 (20)</td>
<td>2.30 (13)</td>
</tr>
</tbody>
</table>

different pelvic classes are shown in Fig. 5. The Kolmogorov-Smirnov Test (Tate and Clelland, 1959) was used to compare the distribution of character states between different pelvic classes within the two samples. Statistically significant results of analysis of the data shown in Fig. 5 and data the means of which are presented in Table 1 are presented in Table 2. Comparisons between the length of the second dorsal spine in fossils of the absent class and the other two classes were not made because the sample size was too small.

*Arrangement of Predorsal Radials and Dorsal Spines*

In normal three-spined individuals of *Gasterosteus*, the first two dorsal spines are anterior to and free from the soft dorsal fin. The smaller third spine is also anterior to but contiguous with the soft dorsal fin. The arrangement of
Figure 5. Histograms of the distributions of character states of meristic characters in the different pelvic morphs of Gasterosteus which tend to reduce or lose the pelvic girdle. A, C, E, G, and I are data for fossils and B, D, F, H, J, and K for Recent, benthic sticklebacks from Paxton Lake. The vertical axes are frequency (%) and the horizontal axes are the number of elements in the meristic series. DEV, developed; VEST, vestigial; ABS, absent pelvic class and N, sample size.
Table 2. Statistically significant results (at the 5% confidence level) of Kolmogorov-Smirnov Test of data presented in Fig. 5 and distributions of dorsal spine lengths, the means of which are presented in Table 1. D, maximum cumulative difference in frequency (%) of character states between two pelvic classes, α, confidence level at which the null hypothesis has been rejected; and Fig., where the data are plotted in Fig. 5.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Character</th>
<th>Classes compared</th>
<th>D (%)</th>
<th>α</th>
<th>Fig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Recent</td>
<td>number of dorsal spines</td>
<td>DEV:VEST</td>
<td>36.37</td>
<td>0.05</td>
<td>5B</td>
</tr>
<tr>
<td></td>
<td></td>
<td>DEV:ABS</td>
<td>27.60</td>
<td>0.05</td>
<td>5B</td>
</tr>
<tr>
<td>Fossil</td>
<td>number of dorsal spines</td>
<td>DEV:VEST</td>
<td>61.16</td>
<td>0.01</td>
<td>5A</td>
</tr>
<tr>
<td></td>
<td></td>
<td>DEV:ABS</td>
<td>66.31</td>
<td>0.01</td>
<td>5A</td>
</tr>
<tr>
<td>Recent</td>
<td>number of dorsal fin rays</td>
<td>DEV:VEST</td>
<td>48.87</td>
<td>0.01</td>
<td>5D</td>
</tr>
<tr>
<td></td>
<td></td>
<td>DEV:ABS</td>
<td>50.34</td>
<td>0.02</td>
<td>5D</td>
</tr>
<tr>
<td>Fossil</td>
<td>number of predorsal radials</td>
<td>DEV:VEST</td>
<td>36.50</td>
<td>0.05</td>
<td>5E</td>
</tr>
<tr>
<td></td>
<td></td>
<td>DEV:VEST</td>
<td>37.57</td>
<td>0.05</td>
<td>5E</td>
</tr>
<tr>
<td>Recent</td>
<td>number of lateral plates</td>
<td>DEV:ABS</td>
<td>37.71</td>
<td>0.01</td>
<td>5K</td>
</tr>
<tr>
<td></td>
<td></td>
<td>DEV:ABS</td>
<td>88.89</td>
<td>0.05</td>
<td>5K</td>
</tr>
<tr>
<td>Fossil</td>
<td>length of third dorsal spine</td>
<td>VEST:ABS</td>
<td>50.00</td>
<td>0.02</td>
<td>—</td>
</tr>
</tbody>
</table>

predorsal radials and dorsal spines forms a complex pattern because the number of both radials and spines varies. I have assumed for the purpose of analysis that the dorsal spines are invariably associated with the same radial and that variation in position is due to addition or loss of radials not bearing spines. Fig 5E and F shows the frequency of different numbers of predorsal radials in different pelvic morphs in the fossil and Recent samples respectively.

Among the fossils, the number of predorsal radials varies from 7 to 1 (Fig. 5E). The modal number of predorsal radials is 5 in developed (61.1%), vestigial (54.8%) and absent (43.5%) pelvic classes. However, 5 is the minimal number of radials for specimens with the developed pelvic girdle, but only 11.8% of specimens with a vestige or lacking the pelvic girdle have greater than 5 predorsal radials. A specimen with 7 radials and 3 spines has the following arrangement:

I II° III° IV V VI VII°

Two-spined specimens (regardless of the number of predorsal radials) lack the spine at II; one-spined specimens lack the spines at II and III; and specimens with no dorsal spines lack the spines at II, III and VII. Specimens with 6 predorsal radials lack IV, V or VI. Those with 5 predorsal radials lack I and IV, I and V, I and VI, IV and V or V and VI. Specimens with fewer than 5 radials could not be analyzed because they have 1 or no dorsal spines. Specimens in the sample with 7 predorsal radials have 0, 1 or 3 dorsal spines; those with 5 or 6 radials 1 to 3 dorsal spines; those with 3 or 4 radials have 0 or 1 spine and those with 1 or 2 radials have 1 spine.
Among the Recent specimens, the number of predorsal radials varies from 5 to 8 (Fig. 5F), but 72.7% of all specimens have 6 predorsal radials. In striking similarity to the fossils, all specimens with a developed or a pelvic girdle intermediate between the typical vestigial and developed pelvic girdle (as in Fig. 2b to e) equal or exceed the modal number of radials (6 or 7) while specimens lacking the pelvic girdle or with only a vestige vary from 5 to 8 predorsal radials. Specimens with 8 predorsal radials and 3 dorsal spines have the following arrangement:

\[ \text{I II III IV}^1 \text{ V}^2 \text{ VI VII VIII}^3 \]

Two-spined specimens lack the spine on radial IV. Specimens with 7 radials may lack II or VI. Those with 6 radials may lack II and III or II and VI. Specimens with 5 radials lack I, II and VI or II, III and VI.

The greater variability of the fossils may be due to poor preservation, since the predorsal radials are delicate structures, easily destroyed in preparation. However, the arrangement of radials and spines in the two samples is fundamentally different.

**Conclusions**

*The Nature of the Samples*

The fossil and Recent samples are very different. The Recent sample is from one population. The fossils came from a series of beds probably representing a span of hundreds of thousands or millions of years. Since the generation time in living freshwater *G. aculeatus* is only one or two years (see Mullem and Vlugt, 1964, for a review of generation time), the fossil collection may represent millions of generations. Thus, the fossil sample of less than 150 specimens represents a very small sample from a very large number of successive related populations. Comparisons of fossil specimens are, in effect, interpopulation comparisons with very small sample sizes. Comparisons of the Recent population are intrapopulation comparisons. Characters correlated with pelvic condition in the fossils may represent correlations of the mean state of the characters in the population to which that individual belonged. The degree to which these characters were correlated within one individual is obscured because the variability of the character in the population to which the individual belonged is unknown. Characters correlated with the pelvic condition in the Recent sample must be due to mechanisms which result in their association in one individual of a population. Possible mechanisms include genetic linkage, strong mortality of phenotypes in which both of the characters are not present, subdivision of the sample into small breeding units (Tabachnick and Underhill, 1972) and pleiotropy. Such mechanisms need not be invoked to explain correlations with pelvic structure of the fossils because they do not represent one population, but such mechanisms may be involved.
The Polyphyletic Origin of Pelvic-less Gasterosteus

The range of variation of the pelvic girdle, lateral plates and the dorsal spines is very similar in the Recent sample from Texada Island and the fossil assemblage from Hazen, Nevada. While there seems to be a suite of correlated characters common to both of the samples, the details of their variation are different. The pelvic structure varies from fully developed to absent with similar vestigial intermediates in both samples. However, fossils with pelvic vestiges tend to have tear-drop shaped vestiges and rarely (1 specimen) have spines. In the Recent sample, pelvic vestiges vary in shape and often have spines.

The number of dorsal spines varies differently in the two samples, although, spines drop out sequentially from first to third in both. In the Recent sample, fewer than 2% of specimens had only one dorsal spine and all had at least one. Fossil specimens with no or one dorsal spine constituted nearly 70% of the sample, even though collecting was biased in favor of specimens with two or 3 dorsal spines. Even in fossils with developed pelvic girdles (which tend to have more dorsal spines, see Fig. 5d), a quarter of the specimens examined had only one dorsal spine. Although lateral plates are reduced in both samples, about 59% of the Recent sticklebacks have 1 to 7 lateral plates on at least one side of the body, but none of the fossils examined had any lateral plates.

The number of predorsal radials and the placement of dorsal spines on the radials differs between the two samples. The maximum number of predorsal radials in the Recent specimens exceeds that of the fossils by one, and the minimum number in the fossils exceeds that of the Recent sticklebacks by 4, although extremely low counts among the fossils may be due to poor preservation. The fossils and Recent specimens that have the same number of predorsal radials always have the dorsal spines at different positions. Predorsal radial and dorsal spine patterns analyzed by Bertin (1925) and Penczak (1962b, 1962c) by techniques similar to those used in this study, differ from the Recent and fossil samples. There is apparently considerable interpopulation and intrapopulation variation in the arrangement of these elements.

Some other differences between the Recent and fossil specimens are, respectively: vertebrae, 30 to 33 (x̄=31.54) and 31 to 35 (x̄=33.32); dorsal fin rays, 9 to 12 (x̄=11.06) and 7 to 10 (x̄=9.03); and anal fin rays, 6 to 10 (x̄=8.56) and 7 to 10 (x̄=8.22). Serial elements of fossils can easily be miscounted because of poor preservation, but this generally results in a lower count than actually existed. The greater maximum of total vertebrae and minimum anal fin rays must represent real morphological differences.

The significance of these morphological differences for the phyletic relationship of the fossil and Recent sticklebacks is difficult to assess. Differences in the number of meristic elements may not have a genetic basis as several are known to be altered by environmental variables such as temperature and salinity (Lindsey, 1962; Lindsey and Harrington, 1972). It seems likely that
differences in the relationship of dorsal spine number and size to pelvic structure, the placement of dorsal spines on the predorsal radials, the form of pelvic vestiges, and the total absence of lateral plates in the fossils represent underlying genetic differences. These morphological differences do not preclude the possibility that the reduction and loss of the pelvic girdle is monophyletic in *Gasterosteus* because random genetic effects such as the founder principle and drift influence subsequent selection, and selection is not a deterministic process.

Whether pelvic loss in *Gasterosteus* has a monophyletic or polyphyletic origin cannot be determined on the basis of only morphological criteria, but zoogeography tends to support the latter possibility. Texada Island, according to McPhail (pers. comm.) was subject to postglacial marine submergence about 5000 years ago. It is reasonable to assume that physiological attributes associated with the trachurus and leiurus phenotypes have been established for a long time because freshwater fossil *Gasterosteus* are all leiurus and the relationship between the physiological and morphological phenotype generally is the same wherever they occur. Thus the sticklebacks on Texada Island must have arrived as the trachurus type. Subsequent selection on the island has produced the pelvic-less phenotype. The fossil sticklebacks are from the Pliocene and were deposited more than 10 million years ago. The absence of low elevation passes from the Lahontan Basin westward to the Pacific Ocean, the ichthyofaunal relationships of the basin, and the presence of *Gasterosteus* in southern California indicate that the fossil sticklebacks probably entered Nevada via river systems draining through southern California before the beginning of the Pliocene. The two samples are separated from each other by great gaps in time and space. The most parsimonius model for the evolution of the lines represented by the fossil and Recent sample is that their advanced features have arisen independently.

**Convergence and Parallelism**

If the morphological similarities between *Gasterosteus* from Texada Island and the Pliocene fossils are independently derived, they may be due to convergence or parallelism. Simpson (1961) has defined the terms parallelism and convergence, and Marshall (1971) has discussed them with respect to the radiation of some teleost fishes. Simpson defines parallelism as "... the development of similar characters in two or more lineages of common ancestry and on the basis of or channeled by characteristics of that ancestry," and convergence as "... the development of similar characters separately in two or more lineages without a common ancestry pertinent to the similarity but involving adaptation to similar ecological status." The definition of parallelism implies that very similar genetic systems which have been inherited from a common ancestor are those that are being selected to produce the parallel phenotypes.

I believe that the close morphological similarity between the fossil and
Recent samples reported in this study represent a case of parallelism. Morphological variation in the two samples is similar and they are relatively closely related. Determination of the genetic basis of the similarity could be achieved only by making genetic crosses, and this is impossible in this case.

**Model For Evolution of Gasterosteus Phenotypes**

Another population of *Gasterosteus* that tends to lose the pelvic girdle has been reported from the Queen Charlotte Islands, British Columbia (Moodie and Reimchen, 1973; Hagen and McPhail, 1970; Nelson, 1971b; Nelson and Atton, 1971) and it was probably also independently derived. The Queen Charlotte population also tends to have reduced dorsal spines (T. Reimchen, pers. comm.). Fig. 6 is a very simplified graphical model

*Figure 6.* Simplified diagramatic three-dimensional plot of the distribution of different *Gasterosteus* phenotypes through time (in years ago) and space (in degrees N latitude). The time axis is logarithmic and the vertical axis is morphological with the primitive phenotype at the bottom. Note that the multiple transitions between structural grades have been limited for clarity and in reality must be much more numerous. The Queen Charlotte Islands population of pelvic-less *Gasterosteus* is not shown.
showing phyletic relationships between *trachurus*, *leiurus*, and pelvic-less structural grades of *Gasterosteus*. Parallelism is probably the dominant mechanism underlying the amphiboreal distribution of *G. aculeatus* with different phenotypes (Băcescu and Mayer, 1956 cited in Münzing, 1963; Hagen and Gilbertson, 1972; McPhail and Lindsey, 1970; Münzing, 1963). Lindsey (1962) reached the same conclusion from studies of the genetic variability of meristic characters in *G. aculeatus*.

Morphological variation upon which selection can act to produce parallel phenotypes is abundant in leiurus populations. Leiurus populations from southern and central California frequently have individuals with reduced numbers of dorsal spines. The maximum frequency of two-spined specimens in leiurus samples examined was about 5%. One sample (LACM 30922-1) with about 5% two-spined individuals also had one one-spined and one four-spined specimen. In the samples in which two-spined individuals were at a high frequency, specimens with the first dorsal spine small and incapable of locking into the normal defensive posture (Hoogland, 1951) were also present in similar abundance. Two, four, and five-spined specimens have been reported from Europe by Penczak (1966). Two-spined specimens are apparently very rare in many European populations (Penczak, 1965). Lindsey (1962) obtained two, three, and four-spined offspring from crosses of three-spined parents. Variation in the number of lateral plates is very well documented in *Gasterosteus* (e.g., Rutter, 1896; Münzing, 1963; Miller and Hubbs, 1969; Hagen and Gilbertson, 1973). Substantial reduction of pelvic structure has rarely been reported (Penczak, 1965).

**Taxonomy**

Determination of the taxonomic categories to which the Texada Island and fossil samples belong is a difficult problem. Mural (1973) assigned the fossil sticklebacks from the Truckee Formation to two species based primarily on pelvic structure, although, he did not describe variation in the pelvic girdle in detail. He believed that Jordan's (1907) type specimen had a normally developed pelvic girdle and restricted *Gasterosteus doryssus* to include only specimens with developed pelvic girdles. He described *Gasterosteus apodus* as a new species of fossil stickleback characterized by vestigial or absent pelvic girdles and reduced numbers of dorsal spines and lateral plates. His data, based in part on specimens used in this study, are largely consistent with my data, but his description of a new species is unwarranted.

Mural suggested several characters to separate the two species of fossil sticklebacks. Individuals with reduced pelvic structures also tend to have fewer dorsal spines than those with a normal pelvic girdle. My data confirm this tendency (Fig. 5A) but this trend is also present in the Recent sample (Fig. 5B) which consists of conspecifics. He also noted that sticklebacks in the University of Michigan Museum of Paleontology collection with normally developed pelvic girdles had “. . . occasionally several lateral plates. . . .” while
those with reduced pelvic structures had "... lateral plates only rarely noted. ..." His conclusion that differences in the frequency of individuals with lateral plates between sticklebacks with different pelvic structure constitute a species character is unjustified. In my Recent sample, individuals (from one population) with reduced pelvic structures were found to have fewer lateral plates (Fig. 5K).

Mural stated that pelvic vestiges in Gasterosteus apodus are always leaf shaped, bilaterally symmetrical, and lack spines. It is true that leaf (tear-drop) shaped vestiges are very common among the fossils, but intermediate pelvic structures occur. Mural examined LACM 17452 which includes 3 individuals and assigned them to G. apodus. These specimens have either developed pelvic girdles (Fig. 3b, c) or a structure intermediate between developed and vestigial (Fig. 4a). LACM 17944A which he considered to be G. apodus has one typical vestige and an intermediate structure (Fig. 4b). Mural also examined Jordan's type specimen (UCMP 9372) and UCMP 9374 and concluded that they have normally developed pelvic girdles. My examination of these two specimens indicated that their pelvic structure closely resembles the intermediate structure of LACM 17944A. Bilateral asymmetry in the size and shape of pelvic vestiges is also present (Fig. 4b, e) and only one pelvic vestige was found in 21 of 67 specimens with vestigial pelvic girdles. CAS 50046 had a much reduced pelvic girdle with spines.

Mural's failure to recognize the degree of pelvic variation in his sample, and his lack of a Recent Gasterosteus population, in which the pelvic girdle may be reduced, with which to compare the fossil sample led him to two incorrect conclusions. He concluded that pelvic variation in his sample differed from intrapopulation variation in Gasterosteus, Pungitius (Nelson, 1971), and Culaea (Nelson and Atton, 1971) which tend to reduce the pelvic skeleton. He believed that the uniform leaf shape structure which he thought characterized pelvic vestiges in his sample constituted a species character. He also concluded that correlations between pelvic structure and dorsal spine and lateral plate number could not occur within one species. These conclusions are refuted by the variability actually displayed among the pelvic girdles of fossils (Fig. 4) and intrapopulation correlation between pelvic structure and dorsal spine and lateral plate number in the Recent Gasterosteus reported in this study (Fig. 5B, K, Table 2). Thus, no evidence has been presented by Mural which would warrant specific separation of fossil sticklebacks with reduced pelvic structure from those with normally developed pelvic girdles. The nominal species, Gasterosteus apodus, is a junior synonym of Gasterosteus doryssus.

The nominal species, Gasterosteus doryssus, should be retained until more data are available on extant populations of Gasterosteus which tend to lose or reduce the pelvic girdle. Nelson (1971b) did not believe that pelvic reduction in Pungitius warranted taxonomic recognition. The criteria of the biological species concept (Mayr, 1963) should be applied to the Paxton Lake
and Queen Charlotte Islands populations. The validity of G. doryssus, a species polymorphic for pelvic structure and other features, may be inferred by analogy with morphologically similar living populations of Gasterosteus.

**DISCUSSION**

*Parallelism Within the Gasterosteidae*

Within the Gasterosteidae, there are three genera, Gasterosteus, Pungitius, and Culaea, which normally have well developed pelvic girdles with an ascending branch and a strong pelvic spine (Nelson, 1971b). In all three genera, there are populations reported with individuals with reduced and missing pelvic girdles. Nelson and Atton (1971) have reported Culaea populations ranging over a wide area in Alberta and Saskatchewan, Canada in which the pelvic girdle tends to be reduced or absent. Although it is possible that these widespread populations represent a monophyletic group dispersed by disruptions of drainage patterns, it is more likely that the unusual morphological attributes of at least several of these populations were independently derived. They occur in different drainages dispersed among normal populations, and postglacial invasion of the area was probably from more than one refugium (Nelson and Atton, 1971).

Pungitius populations in which the pelvic girdle tends to be absent were first reported from Ireland by Day (1878). Nelson and Atton (1971) mentioned populations of Pungitius from Alberta in which about one-third of the individuals had incomplete pelvic girdles. Nelson (1971a) has discussed populations of Pungitius from Ireland and central Canada in which the pelvic girdle tends to be reduced or absent. Coad (1973) reported additional populations in which pelvic reduction occurs at low frequencies (about 5%) from eastern and central Canada. Obviously, parallelism is responsible for at least some of this distribution pattern.

In Gasterosteus reported in this study there is a clear relationship between the condition of the pelvic girdle and the state of several characters. In both samples, there tend to be more dorsal spines in specimens with normally developed pelvic girdles. In the fossils, the third dorsal spine is shorter in sticklebacks lacking the pelvic girdle than in the other two morphs. The second and third dorsal spine may tend to be shorter in fossils with reduced pelvic structures but significant differences were not established. Dorsal spines are about the same length in all Recent specimens. The fossils lack lateral plates but in the Recent sample, specimens with developed pelvic girdles have more lateral plates than those with reduced pelvic structures. Among the fossils, specimens with developed pelvic girdles have more predorsal radials than those with vestiges.

Nelson and Atton (1971) have examined Culaea, and Nelson (1971a) has examined Pungitius to determine if the number of dorsal spines is correlated with the pelvic structure in populations with reduced pelvic girdles. In Culaea, Nelson and Atton (1971) believed that no clear relationship emerges
in interpopulation comparisons between the frequency of reduced pelvic girdles and the frequency of individuals with various numbers of dorsal spines. However, Nelson (1969), studying populations of Culaea with normal pelvic girdles, found that the lengths of the pelvic and dorsal spines were positively correlated. He found that this correlation was stronger between populations than within populations and that the area of pelvic-less populations is where dorsal and pelvic spines tend to be shortest. Nelson (1971b) reported no clear association was found in Pungitius between the condition of the pelvic girdle and the number or size of dorsal spines in interpopulation and intrapopulation comparisons, but pelvic spine length was somewhat shorter in the area of loss of the pelvic girdle in Canada. Day (1878) noted that pelvic-less specimens of Pungitius in Ireland frequently had extreme numbers of dorsal spines. The relationships of the development of these structures in Gasterosteus and of the pelvic girdle and spines in Pungitius and Culaea may indicate that they are responding to a common selection pressure because they may form a complex of defensive structures (Hoogland, et al., 1957).

The Genetic Basis of Parallel Phenotypes of Gasterosteids

Regardless of the selective mechanisms involved in producing the pelvic-less phenotype, a certain set of circumstances has apparently elicited a very similar phenotypic response independently in the genera Gasterosteus, Pungitius, and Culaea since at least the beginning of the Pliocene. The similarity of the normal pelvic structure and of the reduction of the pelvic girdle and dorsal spines in Gasterosteus, Pungitius, and Culaea may indicate that very similar genetic systems involving homologous genes in these genera control the tendency for failure of these structures to develop normally in populations with reduced structures. The portion of the genome upon which selection acts to produce the pelvic-less phenotype has probably been stable since at least the Pliocene and has endured the radiation of the Gasterosteidae. (Genetic homology may also be responsible for the widespread systematic variation in the number of lateral plates of Gasterosteus (Hagen and Gilbertson, 1972)). However, subtle differences in the manner in which the spines and pelvic girdles are reduced in the Recent and fossil samples studied in this paper tend to indicate that there are many genes involved in the formation of defensive structures. Thus, their normal development could be prevented through allelic substitutions at one or more of many loci. Subtle differences in these structures may also indicate the involvement of nonhomologous genes. Rigorous proof of genetic homology in these cases requires that genetic crosses be made. Rarely are such rigorous proofs provided in alleged cases of parallelism. Thus, while the distinction between parallelism and convergence is an interesting one, it is in practice, a difficult one to rigorously demonstrate. It is with this reservation that I apply the term parallelism to variation of defensive structures in the Gasterosteidae.
The degree of genetic homology could be determined by performing interpopulation crosses of congeneric populations and intergeneric crosses between members of the three genera with different pelvic structures. Schwartz (1972) has listed the attempted hybridizations of fishes. He did not list any attempted hybridizations involving Culaea, but he did list several for Gasterosteus x Pungitius. Leiner (1957) was able to produce adult hybrids of Gasterosteus x Pungitius, so it may be possible to cross members of these genera with different pelvic structure. It may also be possible to perform crosses involving Culaea because Apeltes (Moenkhaus, 1911) and Spinachia (Appellöf, 1894) have been crossed with Gasterosteus. Genetic plasticity probably underlies differences in other populations of Gasterosteus characterized by unusual behavioral and morphological adaptations discussed by Hagen and McPhead (1970), McPhead (1969), Moodie (1972a, 1972b), Semler (1971), and Moodie and Reimchen (1973).

Natural Selection For Reduction of Defensive Structures

The selection mechanism for the reduction of defensive structures of gasterosteids is unknown. Nelson and Atton (1971) felt that a disproportionate number of the 20 Culaea populations that they examined which had reduced pelvic structures were less subject to predation than populations with normal pelvic girdles. Hagen and Gilbertson (1972), in a detailed study of the relationship or morphology in G. aculeatus to several environmental variables, found that stickleback populations with a modal number of 7 lateral plates and greater mean pelvic and dorsal spine length were associated with the presence in the habitat of predators on Gasterosteus. Coad (1973) mentioned unpublished studies which yielded the same findings for G. aculeatus in Quebec. Moodie, et al. (1973) found that in the laboratory under winter conditions (short photoperiod and cold water) 7 plated sticklebacks were less subject to predation by salmonids than sticklebacks with 4, 5, 6, 8 or 9 lateral plates. Moodie (1972b) reached a similar conclusion based on stomach content analysis of predatory fishes. Thus, evidence is accumulating that predators act as strong selective agents on spine length and lateral plate number in sticklebacks.

Nelson (1969) has speculated that a reduced number of alternate prey species for predators on Culaea may alter selective pressure on a population because the spines would not discourage predators from exploiting the only available prey. Hoogland, et al. (1957) showed that stickleback spines act as a deterrent to predators, which soon learn to avoid them in favor of alternate prey species. Consequently, alternate adaptations such as streamlining of the body for swifter escape would be selected over increased spination. This hypothesis seems to be applicable to the loss of lateral plates, dorsal spines and pelvic girdles of other sticklebacks. The elucidation of the mechanisms by which predation affects stickleback genomes awaits further research.
Parallelism In Other Groups

Parallelism is responsible for much of the morphological similarity found in sticklebacks in widely scattered but similar habitats. This phenomenon is widespread among organisms. Hubbs (1943) has discussed the case of the Johnny darter, *Etheostoma nigrum*, which occurs in the Great Lakes and Mississippi River basins. Two subspecies, *E. n. nigrum* and *E. n. eulepis* have been recognized. *E. n. nigrum* is wide-ranging and ubiquitous, occurring over sandy bottoms in open water. It is slender and smooth-bodied. *E. n. eulepis* has a restricted distribution and occurs in water congested with vegetation. It is stout and rough-bodied. *E. n. eulepis* occurs in pockets of the appropriate habitat within the range of the other subspecies, *E. n. nigrum*. These pockets of *E. n. eulepis* are apparently products of selection on *E. n. nigrum* populations which have invaded weed choked habitats. Lagler and Bailey (1947) have shown that characters used to separate the two subspecies have a genetic basis in the populations they studied. The phenotypes of the two subspecies are believed to be adaptive for predator avoidance in their normal habitat.

Another interesting example of parallelism in similar but disjunct habitats was discussed by McPhail and Lindsey (1970). *Myxocephalus quadricornis* is a circumpolar species of sculpin which tends to become isolated in fresh water. Compared to the marine form, the freshwater isolates known as *M. q. thompsoni*, have a shorter preopercle spine, lack spines on the head and shoulder girdle and lack tubercles below the lateral line. The degree of divergence in the different characters from the condition in the marine form is always about the same. The transition from marine to fresh water has taken place independently on Arctic islands, in Eurasia and North America (Johnson, 1964). The adaptive significance and genetic basis of the freshwater phenotype is apparently not known.

Hubbs (1940) has mentioned several genera of fishes including *Catostomus, Pantosteus, Gila, Richardsonius, Lepidomeda, Rhinichthys, Cottus,* and *Salmo*, which tend to have parallel isolates.

Kabata and Cousens (1972) studied the structure of the attachment organ, the bulla, of parasitic copepods in the family Lernaeopodidae and found that parallelism has been a dominant feature of the radiation of this group. They recognized three types of bullae: type I of parasites on freshwater teleosts and acipenseriforms, type II of parasites on marine teleosts and type III of parasites on elasmobranchs and holoccephalans. They prepared a phyletic dendrogram for the family based on details of development. The type I bulla occurs in only one group of the family but type II occurs in two independently derived groups plus one early offshoot. Type III bulla also occurs in two distinctive groups. The parallel attainment of the same bulla structure repeatedly has resulted from the responsiveness of bulla structure to host type. The adaptive significance of bulla morphology, the authors speculate, is related to osmotic stress placed on the parasite by the osmolarity of the host tissues and that of the environment.
Mosquin and Small (1971) reported parallel development of autopolyploidy in *Epilobium angustifolium* and *E. latifolium*, members of the primrose family. In both species, diploids occur in more northern and Alpine areas of Eurasia and north America while polyploids occupy warmer, southern regions. Polyploids of both forms closely resemble the diploids except that there is an increase in extra pores in the pollan grains. The two species are closely related and the authors speculated that genetic characteristics of the common ancestral species preadapted them to give rise to autopolyploids. Autopolyploids may have arisen repeatedly within both species.

Geographic variation in the coat color of *Peromyscus* and some other rodents has been shown to be correlated with substrate color (Blair, 1947a, 1947b; Dice, 1939a, 1939b, 1940). Many of these studies included experimental crosses which indicate that coat color is genetically determined. Dice (1947) showed that mice which most closely match the substrate were least subject to predation by visually orienting predators under laboratory conditions. There is strong evidence in some of these studies that coat color has been independently selected to match the substrate in different populations (Blair, 1943, 1947b; Dice, 1939a, 1939b). Many other examples could be cited for the rodents.

Many other cases of parallelism are scattered through the literature. Parallelism for size and shape in the frog genus *Hyla* (Jameson and Richmond, 1971), pigment pattern polymorphisms in the snail *Caepea* (Jones, 1973), and biochemical products in the lichen-forming fungus, *Parmelia*, (Culberson and Culberson, 1973) are a few additional examples. The general pattern that emerges from studies on a heterogenous group of organisms is that phenotypes in a given locality are rather precisely matched by natural selection of existing phenotypes to fit the local environment. Thus, when similar environments are encountered, similar phenotypes for a given species are frequently seen. An alternative explanation for a disjunct distribution of phenotypes is that dispersal has taken place between similar habitats or that populations in these habitats are relicts of a former widespread range. In some cases, parallelism is the only acceptable hypothesis. The distribution of pelvic-less sticklebacks, *Pungitius* (Nelson, 1971a) and *Gasterosteus* are particularly convincing examples of the role that parallelism can play in the distribution of organisms with very similar phenotypes in geographically or temporally separated but ecologically similar habitats. The possibility of parallelism must be considered as a reasonable alternative hypothesis to dispersal or relicts to account for the disjunct distribution of phenotypes within the range of a species. Behnke (1972) did not seriously consider the possibility of parallelism to explain the presence of cisco (*Coregonus pollan*) in Ireland which he believed were not sufficiently different to warrant subspecific separation from the Arctic cisco (*C. autumnalis*) that is not found west of the Menzen River of the eastern White Sea Basin. He concluded that the only explanation for this distribution pattern is that the Irish *C. pollan* populations are relicts of a
widespread postglacial distribution of *C. autumnalis*. This paper contains numerous references to allegedly relictual salmonid populations to explain similarly disjunct distributions of phenotypes. In addition, systematists must be very careful lest they describe as single taxa a series of phyletically unrelated populations which are independently adapted to similar environments. Hubbs, as early as 1929, noted this possibility for *Gasterosteus* and this problem continues to be a source of controversy in this genus (Hagen and McPhail, 1970; Miller and Hubbs, 1969).

**The Law Of Homologous Series In Variation**

If parallelism is an important factor in the distribution of phenotypes within species and closely related species have similar ecological requirements, one would expect to find parallel populations of closely related taxa often in the same areas. This phenomenon was discussed by Vavilov (1922) who termed it the law of homologous series in variation. He gave abundant examples of such series from cultivated plants such as grains, beans, cotton, squash and melons. He concluded that in general, closely related species have similar and parallel series of varieties. The more consanguinous the species are, the more precise is the similarity of the variants. Vavilov believed that a consequence of the law is that one could predict unknown phenotypes from a knowledge of variation in closely related species. Hovanitz (1947) recognized this pattern of parallelism among mosquitoes, fruit flies, and butterflies, and also noted the tendency for parallelism to be more precise among more closely related taxa. The law of homologous series in variation is pertinent to the Gasterosteidae.

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LITERATURE CITED


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