Phyletics and biogeography of the aspinine cyprinid fishes

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Introduction

This study was initiated by the examination of specimens of the Hwang-Ho dace, *Leuciscus mongolicus* (Kessler, 1876) in the collections of the American Museum of Natural History. Even a cursory examination cast doubt on their assignment to the genus *Leuciscus*, and a more detailed anatomical study, reported herein, indicates that the species should be allocated to a new genus. Study of this material has also led to a reappraisal of the genus *Leuciscus* and to a discussion of the phyletics and zoogeography of the aspinine cyprinids.

Methods and materials

As in previous studies (Howes, 1978, 1980, 1981) a wide range of both barbelled and non-barbelled Old World cyprinids have been examined. The materials listed in those papers have been re-examined together with more recently prepared material. In addition, skeletal preparations of many Nearctic taxa have also been studied. The following species were dissected, or skeletal preparations examined.

Abramis brama; *Algansea tincella*; *Aspiolucius esocinus*; *Aspiopsis merzbacheri*; *Aspius aspius*; *Aspius vorax*; *Chondrostoma nasus*; *Elopichthys bambusa*; *Gila bicolor*; *G. copei*; *G. crassicauda*; *G. cypha*; *G. elegans*; *G. nigrescens*; *G. pandora*; *G. robusta* (these include Michigan Museum specimens); *Lavinia exilicauda*; *Leuciscus borysthenicus*; *L. cephalus*; *L. idus*; *L. fellowesii*; *L. lehmanni*; *L. leuciscus*; *L. orientalis*; *L. schmidtii*; *L. smyrnaeus*; *L. souffia*; *L. svallizae*; *L. waleckii* (including the syntypes of *L. waleckii sinensis* in the Swedish Museum of Natural History); *Luciobrama macrocephalus*; *Mylocheilus caurinus*; *Ochetobius elongatus*; *Oreoleuciscus humilis*; *O. pewzowi*; *O. potanini*; *Orthodon microlepidotus*; *Pelecus cultratus*; *Pogonichthys macrolepidotus*; *Ptychocheilus lucius*; *P. grandis*; *P. oregonensis*; *Rhynchocypris variegatus*; *Tinca tinca*; *Tribolodon brandti*; *T. jouyi*; *Xenocypris argenteus*.

The concept of *Leuciscus* and the status of *Leuciscus mongolicus* (Kessler)

The daces and chubs of the genus *Leuciscus* Cuvier, 1817 form the most speciose group of Palearctic cyprinid fishes, there being at least 36 nominal species (the number listed in the BMNH catalogues). The majority of *Leuciscus* species are alike in having moderately deep and stout bodies, broad cranial bones (including the ethmoid and supraorbital), a ventrally directed basioccipital process with a well-formed masticatory plate, biserially arranged uncinate pharyngeal teeth, and a short-based anal fin. Comparative studies (Howes, 1978, 1980, 1981) suggest that these 'diagnostic' characters are plesiomorphic for non-barbelled cyprinids. *Leuciscus,* as presently recognized, cannot be defined by a set of unique characters and is therefore a non-monophyletic assemblage.

One species of '*Leuciscus*', *L. mongolicus* (Kessler, 1876), has, however, a suite of derived characters that sets it apart from the corpus of *Leuciscus* species (detailed in Table I). Some of these specializations are shared with genera of the *aspinine group sensu* Howes, 1978 (see pp. 291 below) and are as follows:

Table 1

Character	*Leuciscus* spp.	*'Leuciscus' mongolicus*
Cranial width	40%	61%
(% of its length from tip of ethmoid indentation to the posterior border of the superaoccipital)	mode of 20 specs representing 6 species (110–230 mm SL)	mode of 9 specs (72–147 mm SL)
Supraethmoid	with slightly concave lateral border	narrow-waisted
Mesethmoid	deep with wide anterior notch	shallow with V-shaped notch
Maxillary mid-lateral ascending process	low	high
Dentary pores	5–6	8
Pterosphenoid	short, lacking shelf and remote from frontal border	elongate, with lateral shelf and extended to the frontal border
Orbitosphenoid keel	deep	shallow
Basioccipital process	ventrally sloped	horizontal
Dilatator fossa	short, sphenotic with straight posterior border	long, sphenotic with concave posterior border
Epioccipital process	short, rounded	extended, triangular
4th infraorbital canal	follows contour of orbit	divergent from orbital border
Operculum	dorsal border short, posterior border rounded	dorsal border long, posterior border concave in outline
Adductor arcus palatini muscle originates from:	parasphenoid and prootic	pterosphenoid, parasphenoid and prootic
Gill-rakers	few, stout and simple	many, slender with a crenate medial membrane
Gap between branchial arch and bucco-pharyngeal roof	restricted (Fig. 11)	extensive (Fig. 11)
Genital papilla	not pronounced	elongate, with deeply folded border

The cranium of *'Leuciscus' mongolicus* more closely resembles that of *Aspius* than that of any other *Leuciscus* species (Fig. 1). This resemblance is due to its narrowness, particularly that of the suprathemoid and the frontals which are markedly concave above the orbit; extension of the posterior border of the epioccipital; extent of the dilatator fossa; width of the pterosphenoid; shallowness of the orbitosphenoid keel and the horizontal plane of the basioccipital process.
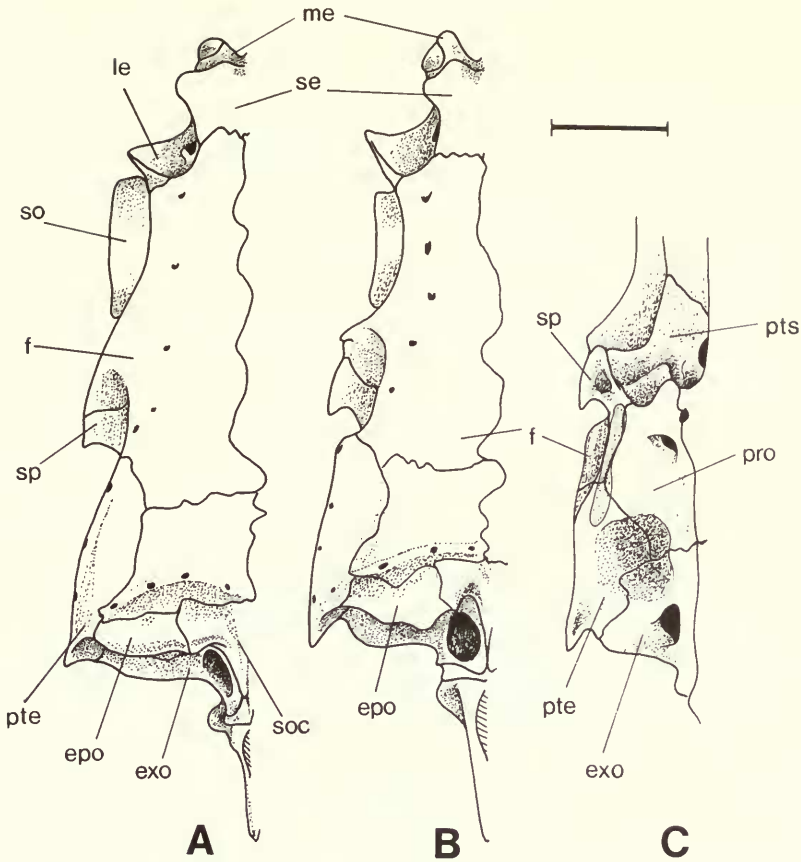
Fig. 1 Crania of A, *Leuciscus leuciscus;* B and C, *Genghis mongolicus.* A and B in dorsal, C in ventral views. Scale = 5 mm. epo = epioccipital, exo = exoccipital, f = frontal, le = lateral ethmoid, me = mesethmoid, pro = prootic, pte = pterotic, pts = pterosphenoid, se = supraethmoid, so = supraorbital, soc = supraoccipital, sp = sphenotic.

Cranial width varies in cyprinids and cannot, by itself, be treated as a synapomorphy. However, among the aspinine genera (*Aspius, Elopichthys, Pseudaspius, Aspiolucius* and *Luciobrama*; Howes, 1978) there is, associated with a narrow cranium, marked concavity of the frontal border above the orbit and an elongate ethmoid region. The lateral margin of the supraethmoid is deeply concave and the mesethmoid arms prominently extended forming a V-shaped anterior notch. All these features are characteristic of '*Leuciscus*' *mongolicus* (Figs 1 & 2).

An aspinine synapomorphy (Howes, 1978) is the posterior extension of the epioccipital which, in combination with the lengthened parietal and flattened lateral portion of the supraethmoid, forms an occipital platform (postcranial platform of Howes, 1978). In '*Leuciscus*' *mongolicus* the occipital platform is not developed to the extent that it is in aspinine genera, but nonetheless this feature is absent in *Leuciscus* species.

The dilatator fossa in '*Leuciscus*' *mongolicus* makes a deep excavation into the frontal (Fig. 1B); the sphenotic is expanded posteriorly with a deeply concave posterior margin. This fossa morphology is unlike that in other *Leuciscus* species where the frontal is only shallowly indented and the sphenotic is short with, at best, a slightly concave posterior border. A long, deep indentation of the frontal and a deeply concave sphenotic are characteristics of the aspinine dilatator fossa (see Howes, 1978, figs 25 & 26).
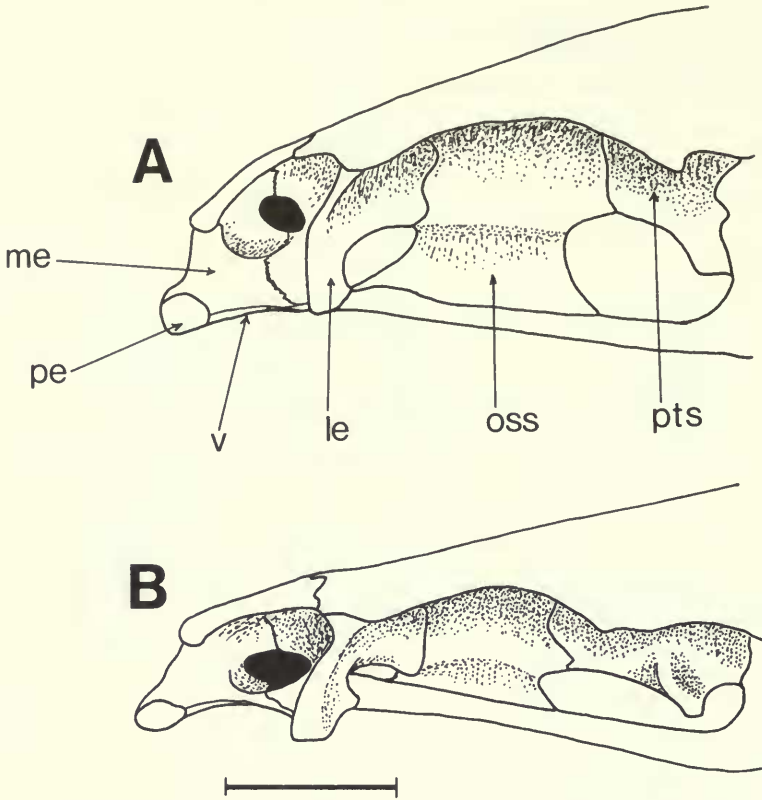
Fig. 2 Anterior cranial region of A, *Leuciscus leuciscus* and B, *Genghis mongolicus* in lateral
views. Scale = 5 mm. oss = orbitosphenoid 'septum', pe = preethmoid, v = vomer; other abbre-
viations as in Fig. 1.

The lateral extension of the pterosphenoid is an aspinine synapomorphy, a feature most
marked in *Aspius* and *Elopichthys*. The most extreme pterosphenoid expansion occurs in
Elopichthys where the bone is also exposed dorsally and forms the site of origin for part of
the *adductor mandibulae* musculature (see Howes, 1978: 32 & 53). In *'Leuciscus' mongoli-*
cus the pterosphenoid is narrowly separated from the margin of the overlying frontal and
resembles the condition in *Aspius* (cf Fig. 1B with fig. 27B in Howes, 1978). As in the aspi-
nine genera, the pterosphenoid is elongate, being longer than the orbitosphenoid and having
a prominent, downwardly curved lateral shelf (Fig. 2B). The usual cyprinid condition is for
the orbitosphenoid and pterosphenoid to be of equal length or for the pterosphenoid to be
shorter and without a lateral shelf. The orbitosphenoids in *'Leuciscus' mongolicus* are joined
to the parasphenoid by a shallow keel or 'septum', thus contrasting with the condition in
other *Leuciscus* species where a deep keel is present (Fig. 2A). Again, this condition
resembles that of the aspinines where contact between the orbito- and parasphenoid is direct
or *via* a shallow keel (see Howes, 1978:31). The anterior myodome in *'Leuciscus' mongolicus*
has suffered reduction as a consequence of the depressed anterior part of the cranium. In
other *Leuciscus* species the myodome is a spacious cavity.

In the arrangement of its infraorbital bones, *'Leuciscus' mongolicus* resembles the
aspinines more closely than it does other *Leuciscus* species (Fig. 3A). Synapomorphic
for aspinine genera is the elongate 3rd infraorbital, the wide separation of the 4th
infraorbital from the orbital border, and its divergent angle (Howes, 1978, fig. 20). In
'Leuciscus' mongolicus there is a similar elongation of the 3rd infraorbital and a divergent
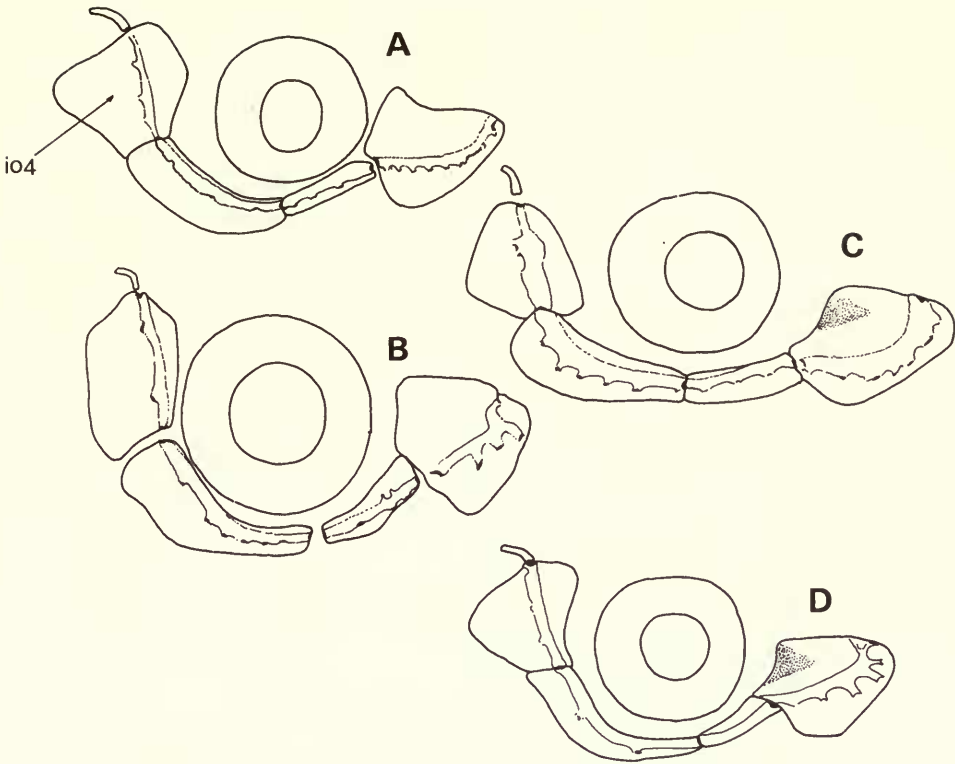
Fig. 3 Infraorbital series of A, *Genghis mongolicus*; B, *Leuciscus leuciscus*; C, *Aspiopsis merzbacheri*; D, *Tribolodon brandti*.

4th element. *Leuciscus* species, in common with most cyprinids, have the 4th infraorbital canal in a near vertical alignment and following the contour of the orbital border (see Howes, 1978, fig. 21). The posterior extent of the bone is variable. What may represent the plesiomorphic condition is illustrated in bariliines (Howes, 1980, figs 29A & B). In these taxa the 4th infraorbital canal also takes a near vertical course and the lamellar part of the bone covers the adductor musculature. In aspinines and 'Leuciscus' mongolicus the 4th infraorbital is also expanded, its posterior margin being attenuated, but the canal runs through the centre of the bone at a divergent angle to the orbit (Fig. 3A). This particular configuration of the infraorbital in the aspinines and 'Leuciscus' mongolicus is a correlate of the elongated posterior cranial bones, particularly the pterosphenoid. The result has been a backward shift of the pterotic-infraorbital canal commissure and a re-alignment of the 4th and 5th infraorbital canals.

The arrangement of the *adductor arcus palatini* (AAP) musculature in 'Leuciscus' mongolicus differs from that of other *Leuciscus* species in having its origin not only from the more usual sites *viz* the prootic and parasphenoid, but also from the pterosphenoid. The anterior part of the muscle originates tendinously from the prominent lateral pterosphenoid shelf and the lateral surface of the parasphenoid ascending process. Insertion of the muscle is on to the lateral face of the posterior margin of the entopterygoid and the entire dorso-lateral face of the metapterygoid (Fig. 4A). The muscle is thick and convex; posteriorly it is confluent with the *adductor hyomandibularis* which runs from the prootic to the medial face of the hyomandibula.

In *Leuciscus* species and the majority of cyprinids, the AAP extends from the base of the neurocranial part of the parasphenoid to its orbital portion. Often, the muscle is continuous with the *adductor hyomandibularis* which originates from the posterior part of the prootic.
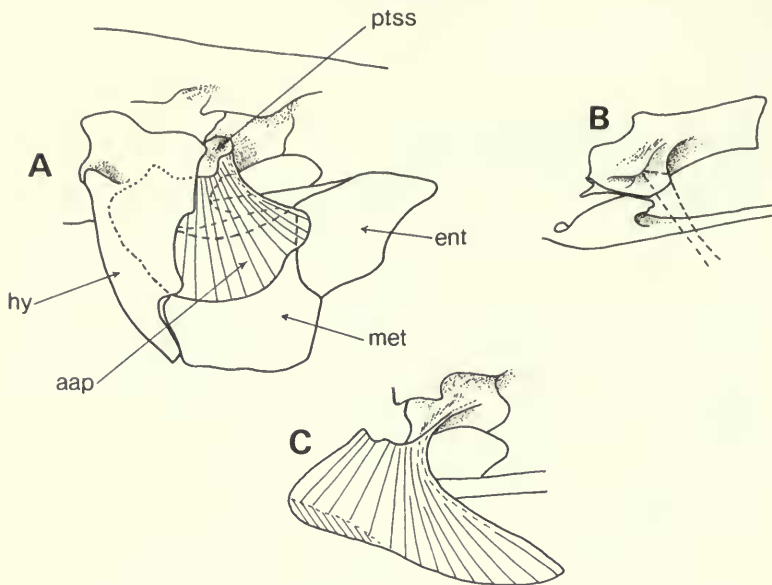
Fig. 4 Origins and insertions of the *adductor arcus palatini* muscle in A, *Genghis mongolicus*; B, *Oreoleuciscus pewzowi* and C, *Pogonichthys macrolepidotus,* lateral views. In A, the dotted line indicates area of origin of the 'adductor hyomandibularis' portion of the muscle from the cranium; the dash-dot line, its insertion on the hyomandibula. In B, the tendinous origin of the muscle is indicated by dashed lines. aap = *adductor arcus palatini* muscle, ent = entopterygoid, hy = hyomandibula, met = metapterygoid, ptss = pterosphenoid shelf.

In cyprinids investigated, only in genera of the aspinine group (except *Luciobrama* which lacks an AAP; see Howes, 1978:24), and in *Oreoleuciscus, Tribolodon* and *Pogonichthys* does the AAP originate from the pterosphenoid. For these taxa the condition is considered to be synapomorphic.

There are 3–4 gill-rakers in *'Leuciscus' mongolicus* on the 1st epibranchial, with 8–9 on the outer and 12 on the inner side of the 1st ceratobranchial. Those on the inner side closely intermesh with the 13 or so rakers on the outer edge of the 2nd ceratobranchial. The gill-rakers are well-developed with a strong, triangular bony spine supporting a thin medial mucosal membrane, the border of which is convex and crenate. The membrane is most developed on the posterior rakers of the ceratobranchial (Fig. 5A). In *Leuciscus leuciscus* and the majority of its congeners, the bony core of the gill-raker is a short, flat, almost equilateral triangle invested by mucosal tissue. This is in contrast to the *'L.' mongolicus* morphotype, where the bony part of the raker is exposed laterally.

Berg's (1949) diagnosis of *Leuciscus* gives gill-rakers as 'short, few (6–30)'; in his key there are three species with more than 13 rakers, *viz. bergi, lindbergi* and *schmidtii*. No specimens of the two former species are available to me, but in *L. schmidtii* the posterior gill-rakers are of the same morphotype as in *'L.' mongolicus*. Gill-rakers with a crenate border to the medial membrane are present also in genera of the *aspinine group* and in *Aspiopsis, Tribolodon, Oreoleuciscus* and *Pogonichthys*. Comprison of gill-raker types in several cyprinid taxa has shown that this form of raker is comparatively rare. Normally the mucosal membrane has a plain concave border, but in some taxa, e.g. *Cyprinus*, the rakers have a thick and highly folded mucosal membrane. Dendritic and pulvinate gill-raker membranes are also common, the tissue often papillose as in abramines. However, in these taxa the pulvinate membrane meets a thick longitudinal septum (see Zander, 1903 for description of *Abramis*) and the rakers lie close together so that the fimbriate medial margins form a sieve.
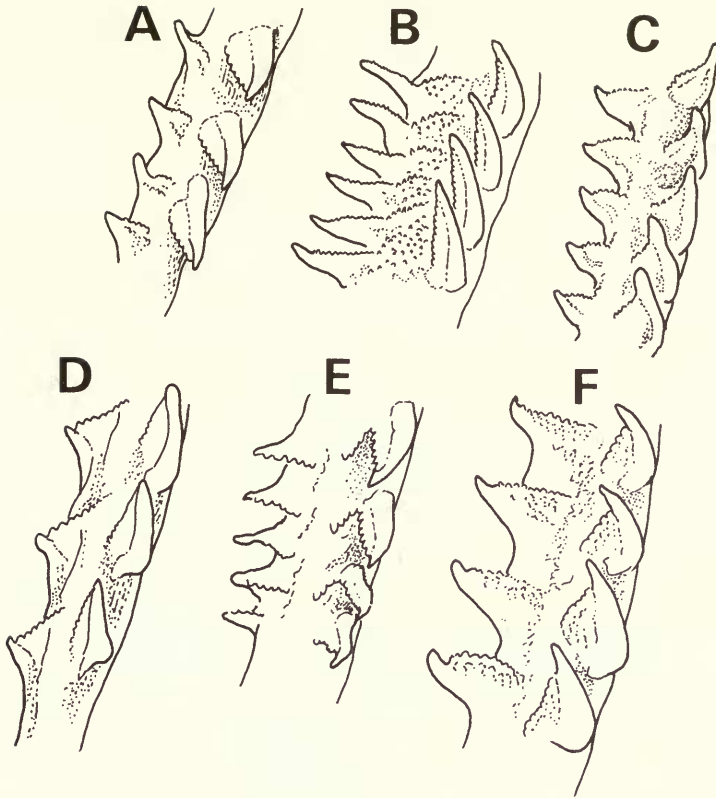
Fig. 5   Gill-raker morphology in A, *Genghis mongolicus*; B, *Oreoleuciscus humilis*; C, *Tribolodon brandti*; D. *Aspius aspius*; E, *Aspiopsis merzbacheri*; F, *Pogonichthys macrolepidotus*. All × 12, except B = × 25. A and E, left, others right 1st ceratobranchial.

Those features analysed above which serve to distinguish '*Leuciscus' mongolicus* from other *Leuciscus* species are specializations shared with genera of the *aspinine group* (see below, p. 291. '*Leuciscus' mongolicus* is, however, excluded from that group since it lacks the three synapomorphies defining it, namely, a high vertebral number, and numerous frontal, nasal sensory pores, and elongated pterosphenoid. As such it is necessary to assign '*Leuciscus' mongolicus* to a new genus:

GENGHIS gen. nov.

TYPE SPECIES. *Squalius mongolicus* Kessler, 1876. *In*: Prejevalsky, N. *Mongolia i strana Tangutov* **2** (4): 21, pl. II. Type locality, Dalai Nor.

ETYMOLOGY. After Genghis (Khan), below whose rampart lies the type locality, Lake Dalai.

DIAGNOSIS. Medium-sized cyprinid fish (the largest specimens measured, 225·5 mm SL), slender-bodied, distinguished from other non-barbelled cyprinids by a combination of the following features: somewhat humped nuchal profile; dorsal cranial profile gently sloped; mouth set obliquely at 45°; border of the 4th infraorbital attenuated and widely separated from the orbit; elongate pterosphenoid, laterally expanded and possessing a lateral shelf from which originates the *adductor arcus palatini* muscle; operculum with attenuated lower posterior border; gill-rakers spinous with crenate medial border; long gape between the branchial arch and pharyngo-buccal roof (Fig. 11); lateral line scales large; caudal fin deeply emarginate.
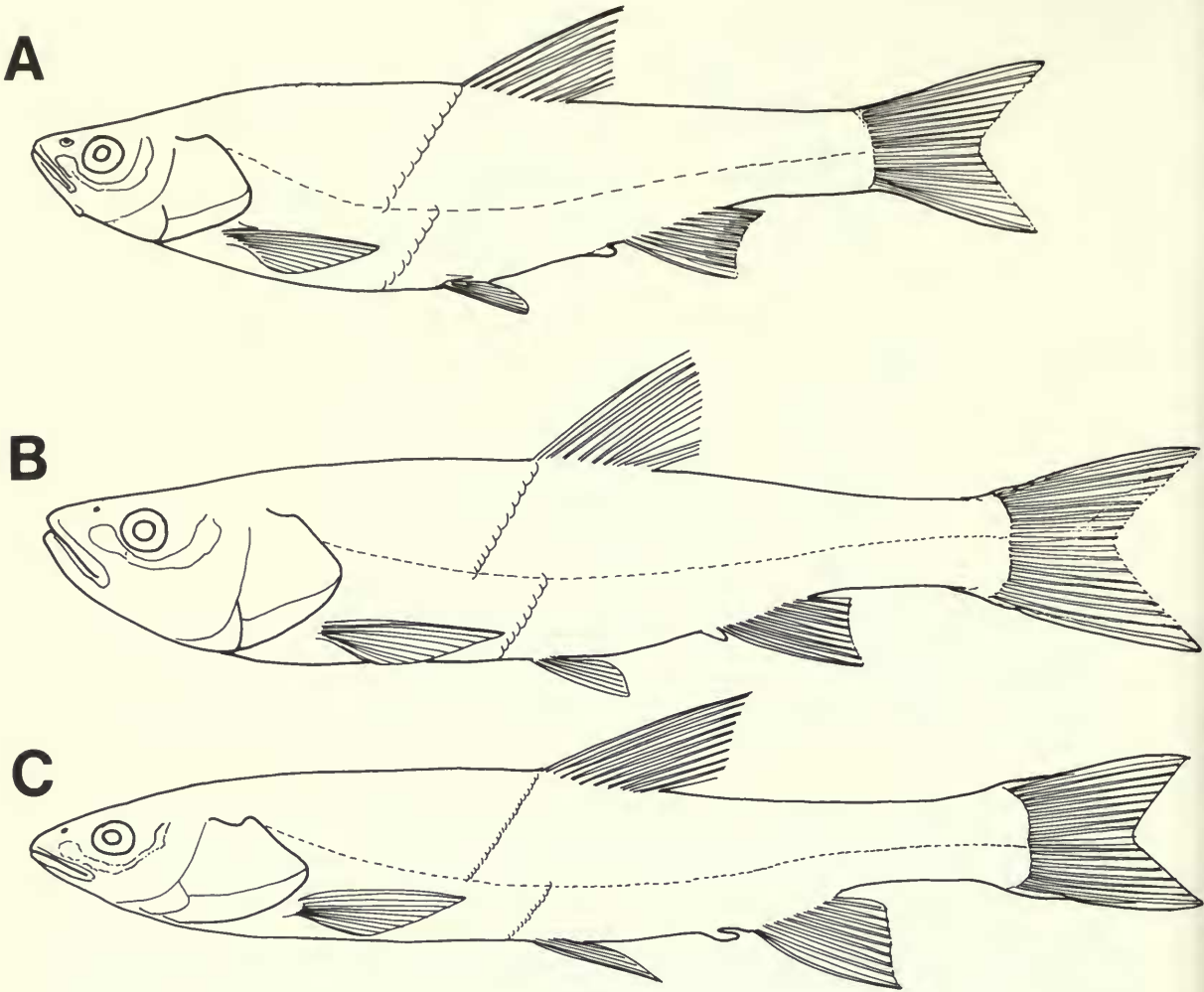
Fig. 6 Outline drawings of A, *Genghis mongolicus*; B, *Aspiopsis merzbacheri*; C, *Oreoleuciscus humilis.*

Genghis mongolicus (Kessler, 1876)
(Fig. 6A)

Squalius chinensis Prejevalski, 1876 *Mongolia i strana Tangutov* **1**: 135 *nomen nudum*
Squalius mongolicus Kessler, 1876. *In:* Prejevalsky, N. *Mongolia i strana Tangutov* **2** (4): 21, pl. II, fig. 2.
Squalius chaunchicus Kessler, 1876 *Ibid:* 23
Leuciscus farnumi Fowler, 1889 *Proc. Acad. nat. Sci. Philad.*: 179
Leuciscus mongolicus, Berg, 1912. *Fauna de la Russie* **3**: 92
?*Leuciscus mongolicus* Oshima, 1926 *Zoological Magazine* **38**: 100
Leuciscus (*Idus*) sp. Miyadi, 1940 *Fishes of Manchuria In:* Hydrobiological Investigations of Kwantung Province and Manchurian Empire: 41, fig. 30.
Leuciscus waleckii suiyuani Mori, 1941 *Zoological Magazine* **53** (3): 183, fig. 2.

NOTES ON SYNONMY *Squalius* Heckel, 1843 is a synonym of *Leuciscus* Cuvier, 1817. Berg (1912: 92 & 110) referred *Squalius mongolicus* Kessler to *Leuciscus* and considered *S. chaunchicus* Kessler a synonym, an opinion endorsed by Bănărescu (1970). Fowler (1899)

described *Leuciscus farnumi* from three specimens, the holotype being from Lake Dalai. Fowler makes no mention of Kessler's species from that lake and his description is undoubtedly that of *mongolicus.*

Oshima (1926) described a new species named as *Leuciscus mongolicus* making no reference to the Kessler species which he had obviously overlooked. Oshima's species was later synonymized by Mori (1934) with *Leuciscus waleckii* (Dybowski, 1869). From Oshima's description it is difficult to tell if his species is Kessler's *mongolicus* or is Dybowski's *waleckii* as was assumed by Mori. Mori's concept of *Leuciscus waleckii* certainly appears to correspond with Dybowski's description of that species, and his illustration shows a fish that is clearly different from Kessler's *mongolicus.* Attempts to trace Mori's and Oshima's specimens have so far failed. Whether or not Oshima's *Leuciscus mongolicus* is synonymous with Kessler's *Squalius* (= *Leuciscus*) *mongolicus*, the fact remains that the name proposed by Oshima is a junior homonym for which I propose, as a *nomen novum, jeholi* as indicative of that species' locality.

Bǎnǎrescu (1970) recognized Mori's (1941) subspecies *L. waleckii suiyuani* as a synonym of *L. mongolicus*, an opinion with which I would concur. I can also confirm Bǎnǎrescu's (1970) opinion that *Leuciscus waleckii sinensis* Rendahl (1925) which also occurs in the Hwang-Ho drainage does indeed belong to that species complex. The possibility that Rendahl's subspecies might also be synonymous with Kessler's *L. mongolicus* has been dispelled by examination of the three syntypes which conform in every respect with Dybowski's *Leuciscus waleckii.*

DESCRIPTION. The following description amplifies that given under the generic diagnosis and is based on the following 18 specimens; AMNH 10907, 4 specs 138–146 mm SL; BMNH 1983.3.1:3–4, 2 specs 130·5; 147 mm SL (ex AMNH 10907); AMNH 10913, 7 specs 72–121 SL: AMNH 10908, 3 specs 93, 106, 145 mm SL; AMNH 10906, 2 specs 154, 222 5 mm SL. All from Paotow (Pao-t'ou), Suiyan Province, Inner Mongolia; collected by C. H. Pope.

As % of SL: body depth 20·1–27·7 (M25·5); head length, 26·2–29·2 (M26·2); caudal peduncle length, 15·9–21·9 (M18·3), caudal peduncle depth as % of its length, 49·2–63·9 (M58·0); as % of head length, interorbital width 24·5–32·0 (M28·8); snout length 21·3–29·6 (M25·7); eye diameter 17·8–23·6 (M22·1); opercular length 29·7–35·5 (M32·9).

Gill-rakers spinous, 3–4 on 1st epibranchial 18–10 on 1st ceratobranchial; extensive gap between branchial arch and bucco-pharyngeal roof (Fig. 12); pharyngeal bones slender, teeth biserial, slender, hooked numbering 5·3 (f3), 4·2 (f1), 4·3 (f2). Scales 9–10/50–52/7–8; Kessler gives a lateral line count of 54 and it is apparent from his figure that he was counting those pore-bearing scales extending onto the base of the caudal fin. Bǎnǎrescu (1970) gives a count of 52–54 for the type specimen of *G. mongolicus.* My counts are those of the standard length. Dorsal fin with III, 7 (f15), III, 8 (f3) rays; anal fin with III, 8 (f2) or III, 9 (f16) rays. Pectoral rays I, 16 (f13), I, 17 (f2), I, 18 (f2), I, 19 (f1); pelvic rays I, 8 (f9) I, 9 (f7).

Swimbladder is two-chambered, the posterior chamber reaching to above the genital opening. Genital papilla prominent with plicate margin. Small pectoral flap and an elongate pelvic axial scale present. Caudal fin emarginate, lobes pointed.

Distribution. The type locality is the lake Dalai (now Hu-lun Ch'ih) in the Nei Monggol, China, 48° N, 117° E; it lies in the plain between the Mongolian Plateau and the Ta Hsing-an-ling Shan-mo (Greater Khinghan) range. According to Berg (1949) there is no outflow of the lake. However, two main rivers flow into Dalai, that from the Mongolian Plateau is the Kerulen (Herlen or Ko lu-lun-Ho) and that from Lake Buyr in the Khingan mountains, is the Orxon (Wu-erh-Shun-Ho). The specimens examined are all from Paotow (Baotaou) on the Hwang-Ho river, some 88° south of the type locality.

Relationships of *Genghis* and the aspinines

The character analysis given above suggests that *Genghis* is closely related to the assemblage of five genera recognised by Howes (1978) as the *aspinine group*, viz.; *Luciobrama, Pseud-*

aspius, Aspiolucius, Aspius and *Elopichthys.* The derived characters uniting these genera are (1) posteriorly and laterally extended pterosphenoid, (2) elongation of posterior cranial bones with development of an occipital platform, (3) unique configuration of the infraorbitals, (4) high vertebral number, and (5) many nasal and frontal sensory pores.

Characters (1)–(3) are possessed by *Genghis* and have already been discussed; (4) and (5) are shared only amongst the *aspinine group* genera, and are discussed below.

Character (4). All aspinines have a total vertebral number in excess of 50 (51–55). Apart from *Pelecus,* with 52 and *Ochetobius* with 61, no other cyprinid has such a high vertebral count (see Howes, 1978). In the aspinines the increase is in the abdominal vertebrae. In three genera, however, namely *Aspius, Elopichthys* and *Aspiolucius,* there is a high number of caudal vertebrae, 22–24 cf. 21 in *Luciobrama* and *Pseudaspius,* a figure that compares with the modal number of other cyprinids viz. 24 (calculated in part from figures published in Howes, 1978, table 1, and from unpublished data). *Pelecus* and *Ochetobius* have both high abdominal and caudal counts. *Genghis* has a total of 45 vertebrae.

Character (5). Aspinine genera share a high number of nasal and frontal sensory pores, respectively 8–10 and 10–22. These counts are unusually high amongst cyprinids; in general the nasal is a short bone with 2–3 pores (exceptionally 6 in some cultrines) and the commonest number of frontal pores is 5–6. Some abramine taxa have 9–10 frontal pores (e.g. *Hypophthalmichthys,* see Howes, 1981 : 17), but the frontal morphology of the abramines and their recognition as monophyletic on the basis of other synapomorphies, suggests an independent derivation of increased sensory pore numbers. High numbers also occur in *Oreoleuciscus* (see below) and in species of the Nearctic genera *Ptychocheilus, Gila, Lavinia* and *Pogonichthys.* These genera, as is the case with aspinines, tend to have elongate crania and it may be that increased pore number is a straightforward correlation with cranial length. This does not always follow, however, since many cheline, bariliine, cultrine and schizothoracine taxa also have lengthened crania but show no sign of an increase in frontal pore number. By itself it would be dubious to treat a high frontal pore number as synapomorphic but in combination with increased numbers of nasal and mandibular pores it seems a valid synapomorphy for aspinine taxa. Whether this is also the case for the high frontal pore number in the Nearctic taxa demands further investigation.

A character overlooked by Howes (1978) when considering aspinine group synapomorphies is the extreme development of the coronomeckelian bone. The usual cyprinid condition is for the bone to be small and irregularly shaped, with a medial shelf on to which inserts the tendon of muscle A_2. Among the aspinines, the coronomeckelian bone of *Luciobrama* is the most derived, being a long, almost boomerang-shaped element with a wide medial shelf (Fig. 7C). In *Elopichthys* the coronomeckelian has an irregular shape but with a long anterior process. The shape of the bone in *Aspius* is most like that of *Genghis,* being broadly triangular with a wide medial shelf (Figs 7A & B). Departure from the general cyprinid condition also occurs in *Tribolodon, Oreoleuciscus, Pogonichthys* and *Ptychocheilus* where it is long and triangular (Figs 7D–F). A similarly shaped bone is present in some *Phoxinus* species. The value of this character is difficult to judge, as its development may be related to the insertion of the adductor muscle. From the various teleost jaws figured by Nelson (1973) it seems that there is much variability in the size of the coronomeckelian; in some plesiomorphic groups (e.g. gonorynchids, esocoids, amiids) the bone appears insignificant, whilst in others (hiodontids, albulids, argentinoids) it is extensive. All that can be said is that in aspinines and the other taxa considered above, the coronomeckelian is of a particularly unusual (and possibly derived) shape which may represent a synapomorphy.

The relationships of *Genghis* plus the aspinines must now be considered. Howes (1978) thought *Oreoleuciscus* (Fig. 6C) the most likely candidate as the sister group of the aspinines. It is now clear that this is not the case since *Oreoleuciscus* possesses none of those characters uniquely shared by *Genghis* and the *aspinine group.* Nonetheless, *Oreoleuciscus* has a close affinity with these taxa as it shares with them and with *Tribolodon* both an elongate pterosphenoid bearing a lateral shelf from which originates part of the *adductor arcus palatini* musculature, and crenate gill-rakers. The configuration of the infraorbitals in *Oreoleuciscus*
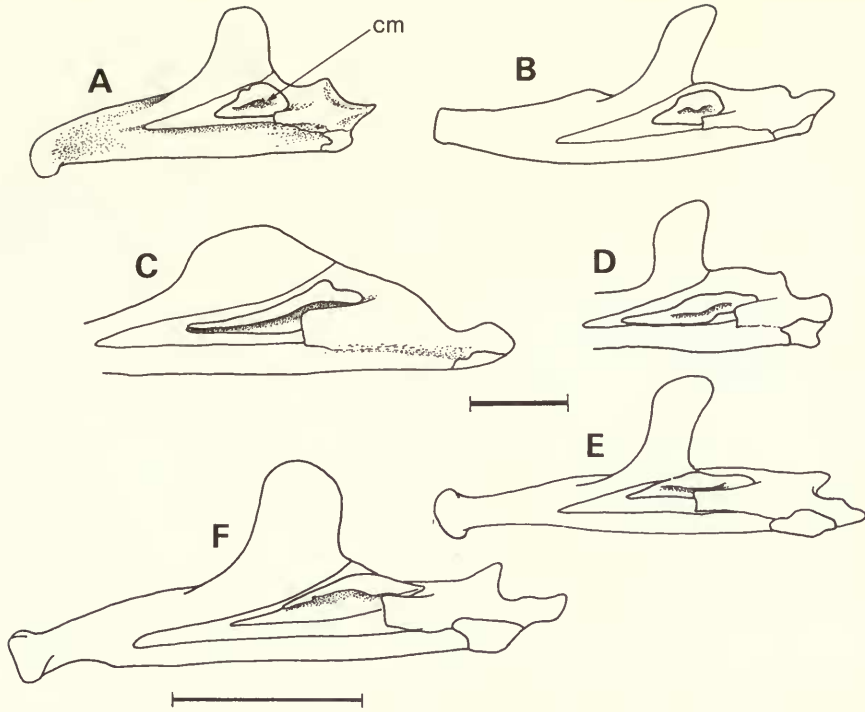
Fig. 7 Lower jaws, medial views to show coronomeckelian bone (cm) of, A, *Genghis mongolicus;* B, *Aspius vorax;* C, *Luciobrama macrocephalus;* D, *Oreoleuciscus humilis;* E, *Pogonichthys macroleptidotus*; F, *Tribolodon brandti.* Scales = 5 mm.

resembles that of the aspinines and *Genghis* in that the 3rd infraorbital extends, almost horizontally, well past the posterior border of the orbit with a consequent separation of the 4th infraorbital from the orbital margin. However, the 4th infraorbital is reduced to its canal tube and is not diagonally aligned, as in the aspinines and *Genghis* (cf. Figs 3A, C & D with fig. 22 in Howes, 1978).

A simple sister-group relationship between *Oreoleuciscus* and *Genghis* plus the aspinines is disrupted by the monotypic genus *Aspiopsis* (Fig. 6B). Only a single syntype is available for examination and only those characters visible without dissection and from radiographs can be ascertained. Howes (1978 : 60) followed Berg (1949) in considering *Aspiopsis* to be synonymous with *Leuciscus,* but a reappraisal of *Aspiopsis* makes it clear that it is a distinct genus and must be included amongst the assemblage of genera discussed here.

Aspiopsis is characterized by a rather elongate body, an operculum with attenuated posterior border, small, imbricate scales (70 in the lateral line), numerous gill-rakers (27 on the 1st ceratobranchial) with a crenate medial membrane, and a papillate lateral buccal membrane, particularly over the preopercular area adjacent to the gill-arch. Radiographs reveal an elongate cranium. In the shape and configuration of its infraorbitals, *Aspiopsis* closely resembles *Genghis* and the aspinine genera (Figs 3C). The 1st infraorbital, however, bears a V-shaped depression on its dorsal margin, a feature encountered elsewhere only in *Tribolodon.* In these characters, apart from the latter, *Aspiopsis* most clearly resembles *Oreoleuciscus.* Lack of dissectable material precludes investigating the site of origin of the *adductor arcus palatini* muscle in *Aspiopsis.* Assuming that this muscle does originate from the pterosphenoid, then *Aspiopsis* would be considered as the sister-lineage to *Oreoleuciscus.* On the basis of their cranial elongation *Aspiopsis* and *Oreoleuciscus* appear most closely related to *Genghis* and the aspinines; however, the derived 1st infraorbital morphology which
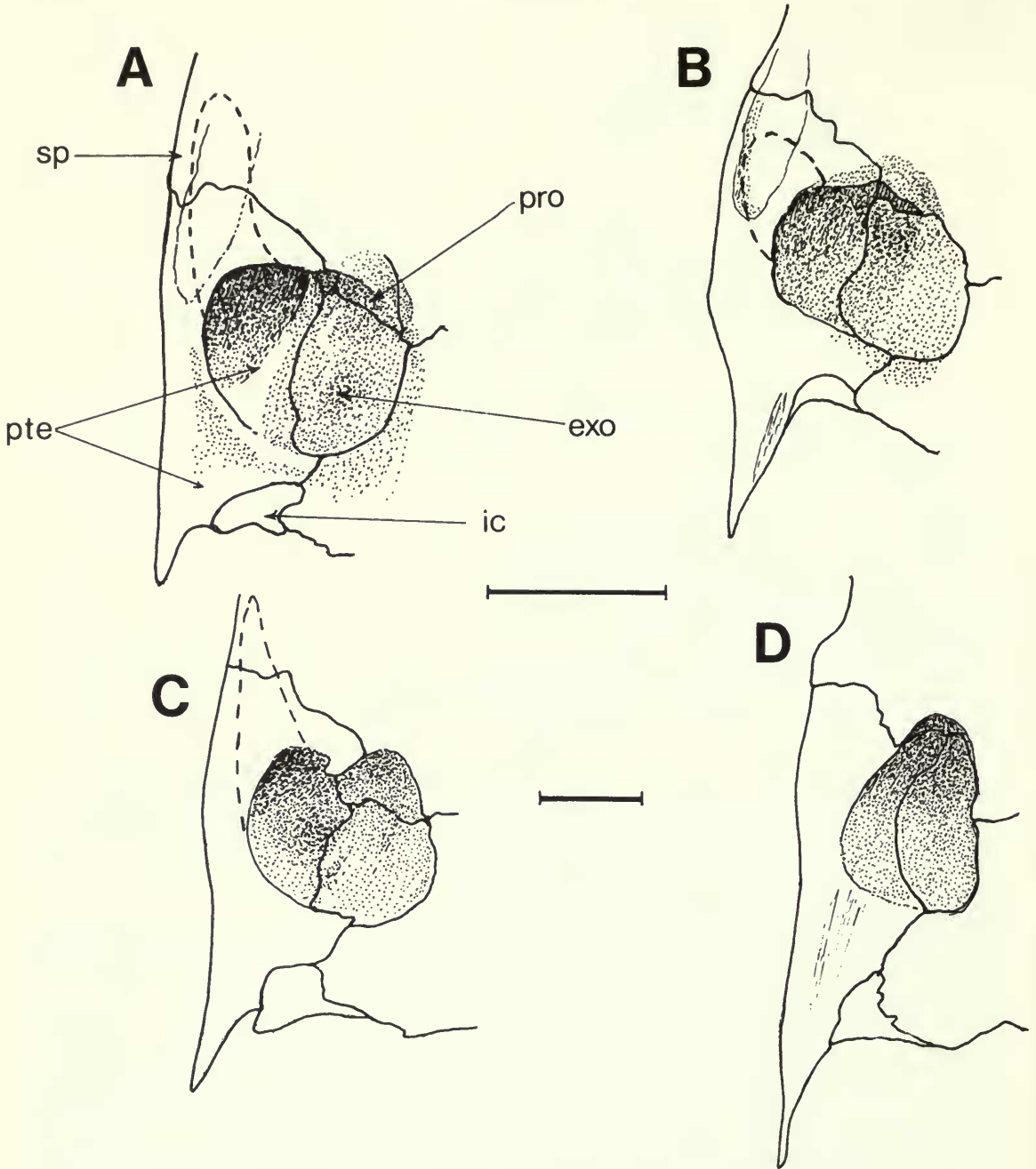
Fig. 8   Subtemporal fossae of A, *Tribolodon brandti;* B, *Ptychocheilus oregonensis;* C, *Pogonichthys macrolepidotus;* D, *Aspius vorax,* dashed lines indicate extent of the anterior chamber.

Aspiopsis shares with *Tribolodon* places the *Aspiopsis–Oreoleuciscus* lineage in an unresolved trichotomy, with *Genghis* and the aspinines on the one hand, and *Tribolodon* on the other. The trichotomy may be resolved when the anatomy of *Apsiopsis* is better known.

   Tribolodon, as well as sharing a derived infraorbital feature with *Aspiopsis* also shares with the aspinines, *Genghis, Oreoleuciscus* and the Nearctic genus *Pogonichthys,* a pterosphenoid
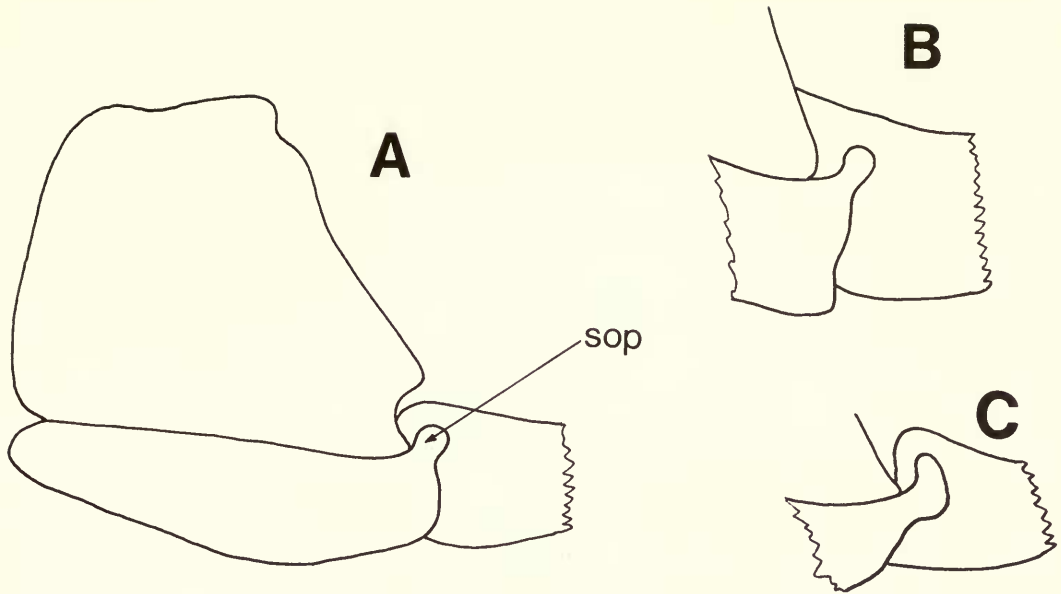
Fig. 9   Suboperculum, medial views showing anterior process (sop) of A, *Tribolodon brandti;* B, *Pogonichthys macrolepidotus* (210 mm SL); C, *Ptychocheilus grandis* (UMZM 181 929–5, 315 mm SL).

origin of the *adductor arcus palatini* muscle, crenate margined gill-rakers, and a triangular coronomeckelian bone. In addition, *Pogonichthys*, shares with *Tribolodon* a derived form of subtemporal fossa, suboperculum and caudal skeleton as follows:

The *subtemporal fossa* in *Tribolodon* and *Pogonichthys* has an anterior extension into the autopterotic and sphenotic (Fig. 8). The extension is in the form of a narrow, finger-shaped chamber filled with a plug of fat. A sphenotic contribution to the subtemporal fossa was recognized by Howes (1982) as a synapomorphic condition for an assemblage of barbelled carps, named the *squaliobarbine group*. In these taxa however, the subtemporal fossa has a different shape in that the fossa is more extensive, with the prootic and exoccipital contributing substantially to its roof. Furthermore, in the squaliobarbines, part of the *levator posterior* muscle originates from the sphenotic chamber. In *Tribolodon* and *Pogonichthys* the *levator posterior* takes its origin dorsally from the pterotic and epioccipital only, and posteriorly from the exoccipital—as in the case of *Cyprinus* shown by Eastman, 1971—, the sphenotic is not involved. This particular type of fat-filled sphenotic chamber in *Tribolodon* and *Pogonichthys* has not been discovered in any other cyprinid examined. In *Ptychocheilus,* there is a lateral cavity of the subtemporal fossa in the pterotic and this too contains a fatty plug (Fig. 8). Amongst the aspinine genera the subtemporal fossa is small and trianguloid in outline (Fig. 8).

The *suboperculum* in *Tribolodon* and *Pogonichthys* has a club-shaped antero-dorsal process (Figs 9A & B). Normally this part of the bone is rounded, or, if produced, it is in the form of a slender triangle. A similarly shaped subopercular process also occurs in *Ptychocheilus* (Fig. 9C).

The *caudal skeleton* in *Pogonichthys* and *Tribolodon* exhibits hypertrophy of the preural neural spines. In *Pogonichthys* the neural spines of the 2nd-4th preural centra are thickened and antero-posteriorly lengthened and articulate distally with hypertrophied procurrent rays (Fig. 10A). In *Tribolodon* the 2nd and 3rd preural neural spines bear prominent anterior lamellae (Fig. 10B). Cyprinids are generally conservative in the morphology of the caudal skeleton and hypertrophy of the preural neural spines is rare. Often, however, there is a
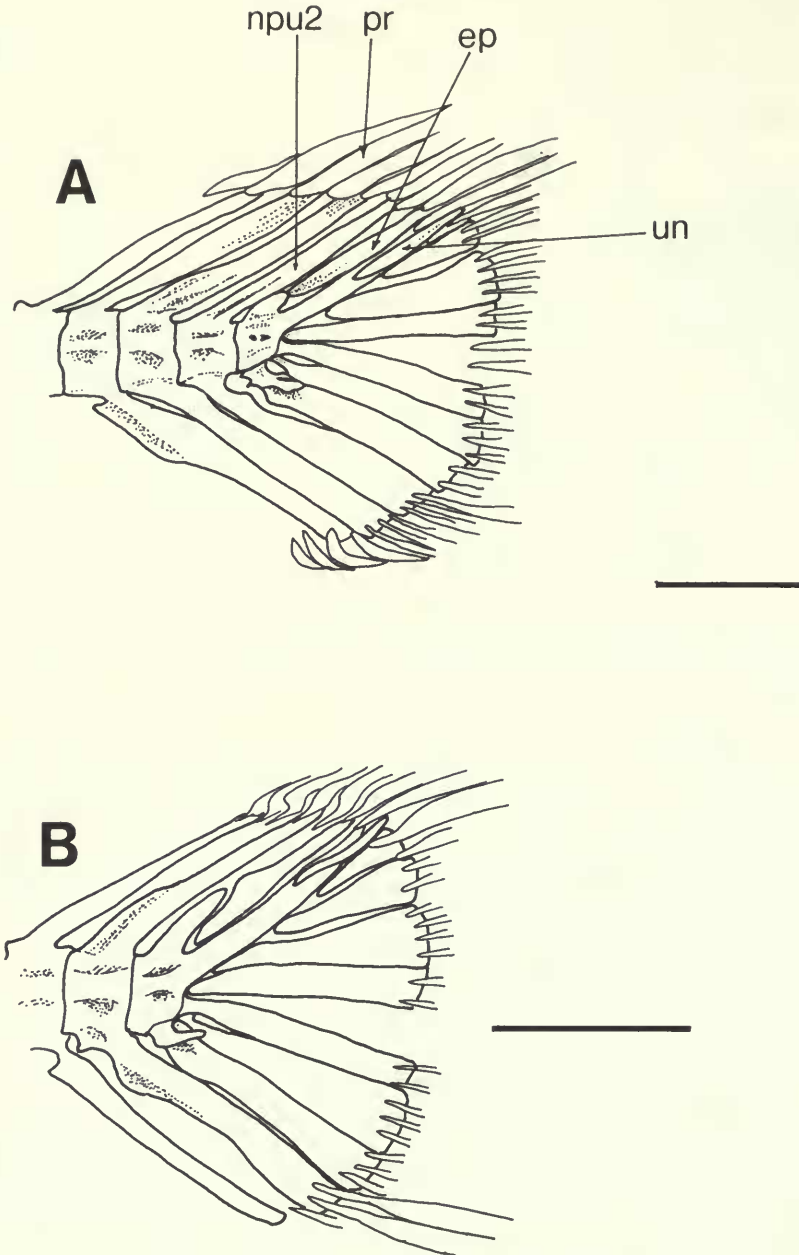
Fig. 10   Caudal skeletons of A, *Pogonichthys macrolepidotus;* B, *Tribolodon brandti;* ep = epural,
pr = procurrent ray, npu2 = neural spine of 2nd preural vertebra, un = uroneural. Scales = 5 mm.

double neural spine on the 3rd preural centrum, and this feature regularly occurs among
aspinine species. It is possible that the hypertrophied condition of the spines in *Tribolodon*
and *Pogonichthys* is due to coalescence of the spines into a single unit. The Nearctic genera
Ptychocheilus and *Lavinia* also display thickening of the preural neural spines and *Lavinia*
has hypertrophied dorsal procurrent rays, a feature shared with *Pogonichthys*. There is
further evidence to suggest *Pogonichthys* and *Ptychocheilus* have close phylogenetic links.

Ptychocheilus shares with *Tribolodon* and *Pogonichthys* the club-shaped subopercular anterior process (see above & Fig 9). *Ptychocheilus* also has crenate and papillate gill-rakers. In *Ptychocheilus oregonensis* the anterior fibres of the *adductor arcus palatini* muscle originate from the lower part of the pterosphenoid, but there is no prominent pterosphenoid shelf like that in *Pogonichthys*.

The cladistic relationships of the Nearctic 'aspinines' *Pogonichthys* and *Ptychocheilus* have yet to be ascertained. Apparent synapomorphies linking *Ptychocheilus* with the Nearctic genera *Mylopharodon* and *Gila* (part) have been reported. Hopkirk (1973) pointed out the similarity of jaw and gill-raker structure with *Mylopharodon* and Illick (1956) drew attention to the looped canal on the 1st infraorbital in both *Ptychocheilus* and *Gila robusta*. According to Illick (1956) this canal configuration does not exist in other Nearctic taxa and I have not found such an erratic course of the canal in any Old-World cyprinid taxon.

To summarize; *Genghis* represents the sister lineage of the aspinine genera, *Aspius*, *Elopichthys*, *Pseudaspius*, *Aspiolucius* and *Luciobrama,* which in turn from one part of a triad whose two other lineages are *Aspiopsis* + *Oreoleuciscus* and *Tribolodon* + *Pogonichthys*. It cannot as yet be determined which of these two lineages is the closest relative of *Genghis* and the aspinine group. This impasse is expressed as an unresolved trichotomy in the cladogram (Fig. 12).

Now that the *aspinine group sensu* Howes (1978) are seen to form one part of a more extended monophyletic assemblage, it is necessary to broaden the concept of the *aspinine group* so as to embrace *Genghis, Aspiopsis, Oreoleuciscus, Tribolodon* and *Pogonichthys*. The wider relationships of the aspinines are presently unclear. However, in discussing the characters which distinguish '*Leuciscus*' *mongolicus* from other *Leuciscus* species it was noted that two species, *L. lehmanni* and *L. schmidtii* possess a gill-raker morphology similar to that of *Genghis mongolicus*. Furthermore, these two species have an extensive gap between
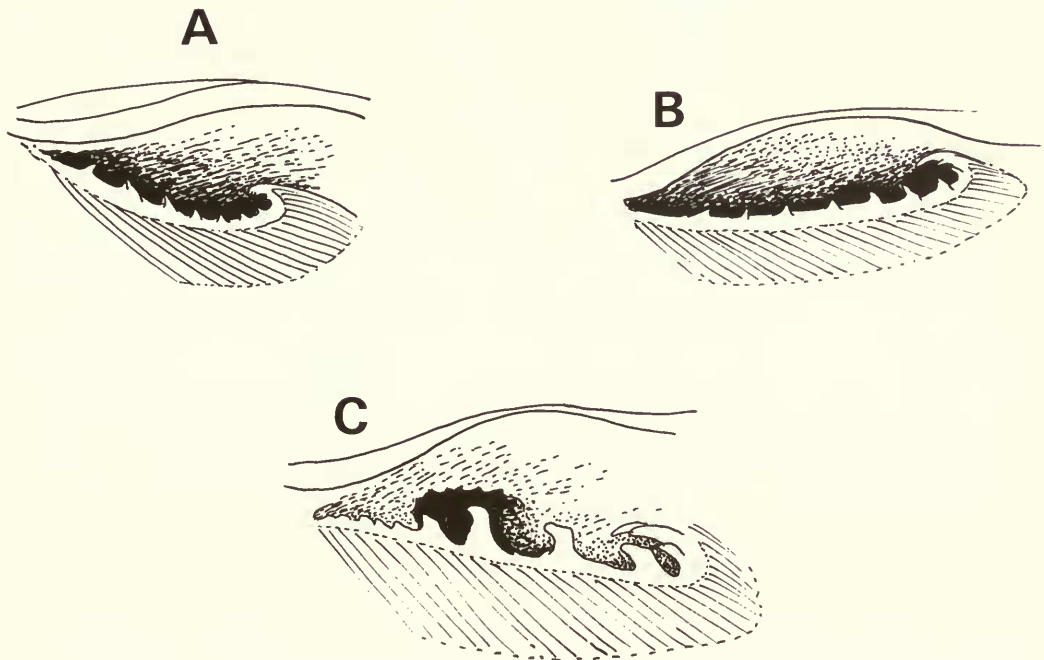

Fig. 11   Ventral view of 1st gill-arch (operculum raised) to show extensive opening between it and the bucco-pharyngeal roof in A, *Genghis mongolicus* and B, *Aspius aspius*, and the restricted opening in C, *Leuciscus leuciscus*.
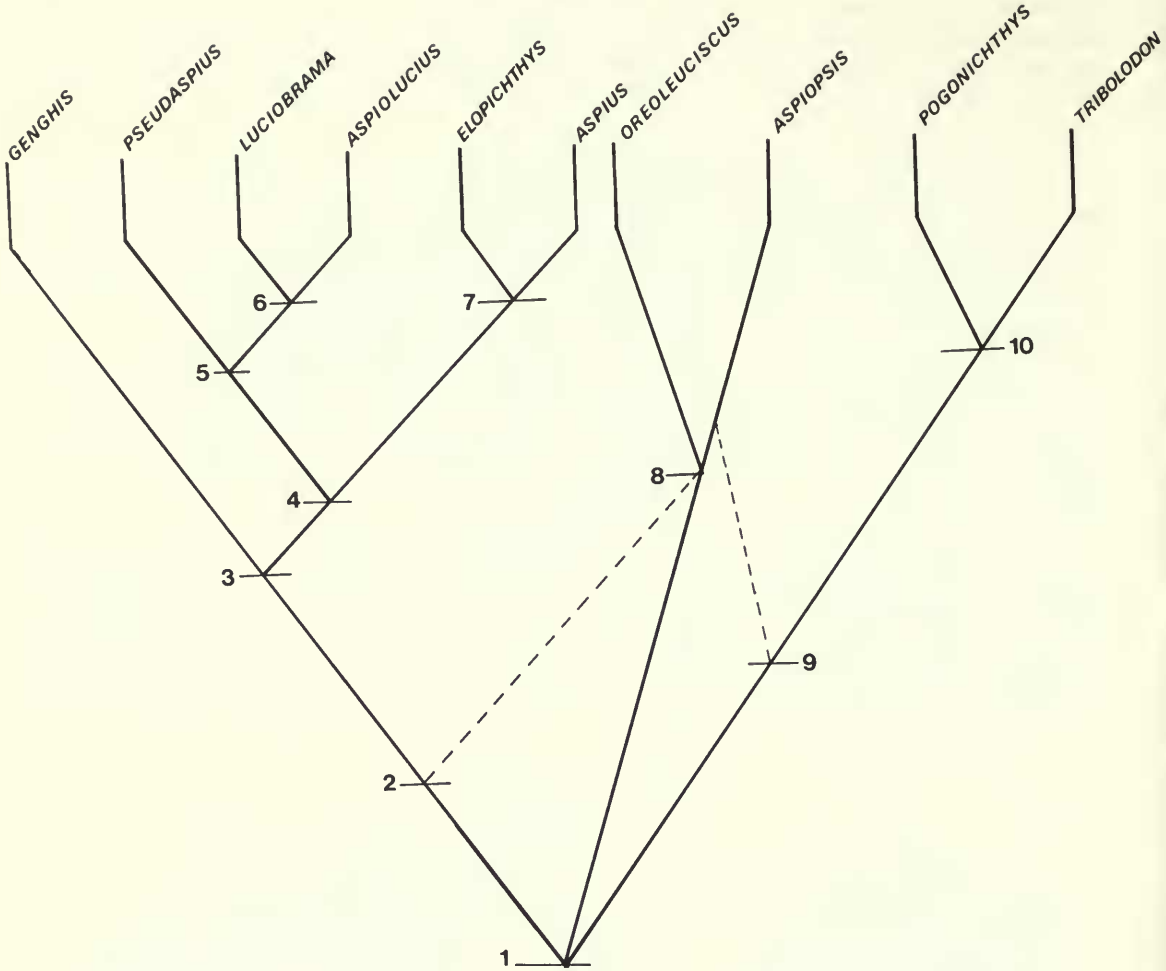
Fig. 12 Cladogram depicting the hypothesized relationships of the *aspinine group.* Synapo-
morphies: (1) Crenate margined gill-rakers; AAP muscle originates from pterosphenoid shelf;
elongate, triangular coronomeckelian bone (this character of dubious polarity). (2) Derived
infraorbital configuration; elongate posterior cranial bones. (3) Further derived state of
infraorbital morphology; well-formed occipital platform; elongate and laterally expanded ptero-
sphenoid. (4) Vertebrae 51–55; extensive contact between pterosphenoid and parasphenoid;
nasals elongate with 6–10 pores. (5) Elongation of occipital region and lower jaw; tunnel-like
post-temporal fossa. (6) Extreme divergence of 4th and 5th infraorbital canals; elongation of
ento- and metapterygoid; complex development of LAP muscle. (7) Extensive aortic foramen
in basioccipital process; 13–16 supraneurals. (8) Papillate lateral buccal membrane; attenuated
operculum. (9) Concavity of 1st infraorbital (shared only with *Tribolodon*). (10) Club-shaped
subopercular process; hypertrophy of preural neural spines.

the branchial arch and pharyngo-buccal roof, in contrast to the restricted space of other
Leuciscus species (Table 1 & Fig. 11). It seems likely that '*Leuciscus' lehmanni* and '*L.'*
schmidtii (both from Central Asia) may represent the sister group to the aspinines, and that
the whole assemblage is the sister group to an, as yet, unidentified monophyletic unit within
the all-embracing '*Leuciscus'*. These ideas can only be tested by a revision of '*Leuciscus'*
(see comments below in Conclusion section).
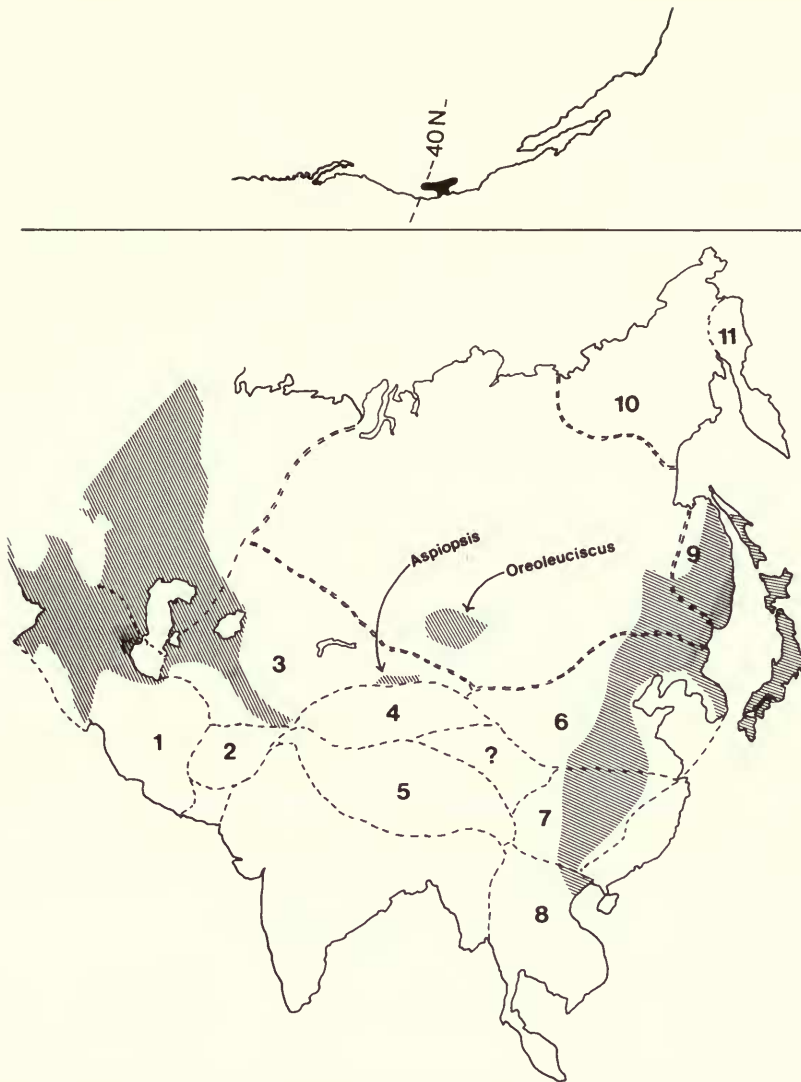
Fig. 13 Distribution of the *aspinine group* in Asia (hatched, below) and western North America (solid black, above). The numbered zones on the Asian map refer to the disposition of accreted continental plates as proposed by McElhinny *et al.* (1981) and Leith (1982). Double-dashed lines indicate the boundary of the Siberian craton. Plates; 1 = Iranian, 2 = Afghanistan, 3 = Kazakh-stanian, 4 = Tarim, 5 = Qinhai-Tibet, 6 = Sino-Korean, 7 = Yangtze, 8 = SE Asian, 9 = Sikhote Alin, 10 = Kolyma, 11 = Kamchatka. Map of Asia drawn on Zenithal equal-area projection.

Biogeography of the aspinines

Distribution within Asia

The most significant feature of aspinine distribution within Asia is its east-west dichotomy (Fig. 13). *Aspius* lies to the west, covering much of Europe and extending south to the Tigris. *Aspiolucius* occurs sympatrically with *Aspius* in the Amu Darya (see Coad, 1981). The majority of aspinine genera are distributed east of the Mongolian plateau; *Elopichthys,* the
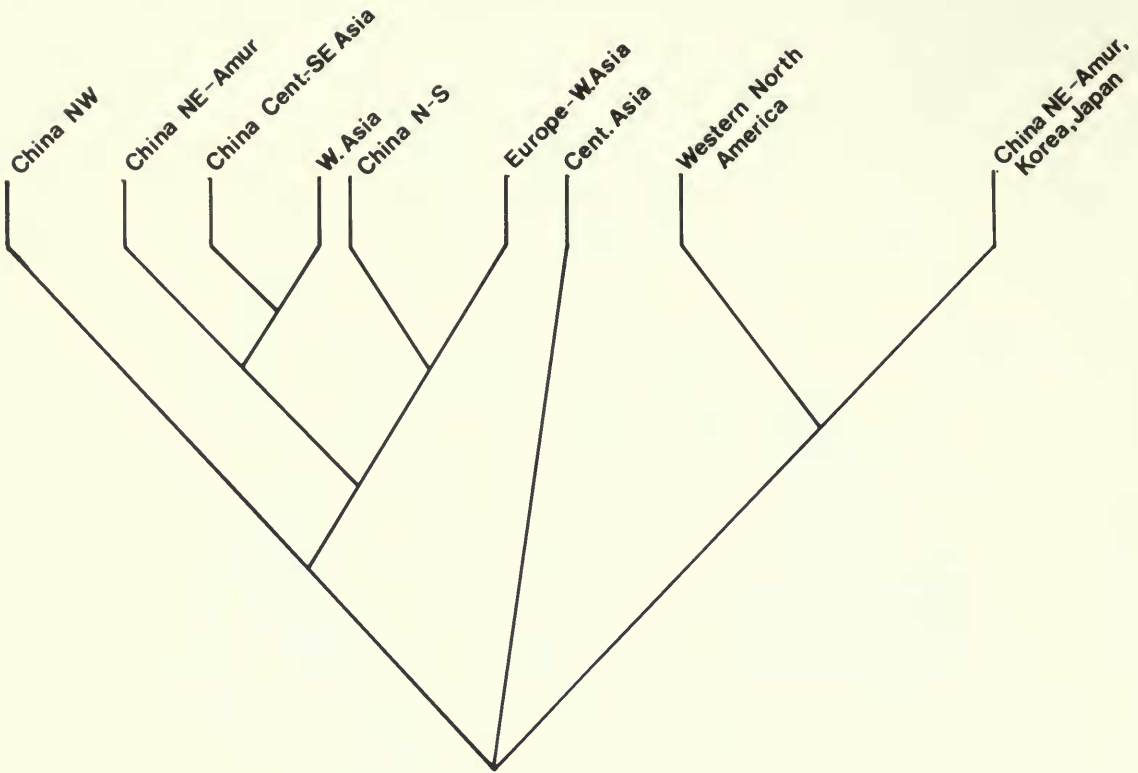
Fig. 14   Area cladogram of the aspinine group.

sister genus of *Aspius; Pseudaspius* and *Luciobrama*, the relatives of *Aspiolucius*, all lie
in the Sino-Korean region (including the Amur; the Siberian and China subregions of Mori,
1936). *Luciobrama* extends south to Hanoi. The plesiomorphic aspinines, *Genghis* and *Tribolodon* also occur in eastern Asia. The former in northern China and the latter along the
coastal margin of the Yellow Sea and the Sea of Japan and the Pacific coasts of Japan and
Sakhalin. Only two genera, *Aspiopsis* and *Oreoleuciscus* occur in Central Asia, being confined, respectively to a small area bordering Sinkiang and the landlocked basins of the Upper
Ob and Bya in Mongolia.

An area cladogram of the Asian aspinines shows a repeated dichotomy in the two lineages
between western and eastern Asia (Fig. 14). The lineage of central Asian genera forms part
of an unresolved trichotomy with the East Asian and Japanese–American branches and so
is uninformative as to its area relationships.

Trans-Pacific links

The phyletic relationships established here between *Tribolodon* and *Pogonichthys* supports
the hypotheses of Miller (1959; 1965), Hopkirk (1973), Gosline (1974) and Howes (1980)
that a close relationship exists between some western North American and Japanese and
Chinese cyprinid taxa. This Pacific link is the only one so far known for members of the
Cyprinidae, although a well-known relationship exists elsewhere within cyprinoids, namely
that between Chinese and American catostomids (see Patterson, 1981). The area cladograms
presented by Patterson (1981) for various Nearctic and Palearctic freshwater teleosts, suggest
closer links between western-North America and eastern America and Europe than with
Asia.

Links between eastern Asia and western-North America are, however, forthcoming from cladistic relationships established amongst various insect groups. Ross (1974) demonstrates a Pacific link for caddisflies and Edmunds (1981) in discussing the distribution of mayflies points to the relationships between Eurasian and Nearctic genera as displaying strong Pacific vicariant patterns. Tuxen's (1977) analysis of proturans points out an 'unexplained' geographic relationship between Japanese and a Nearctic species of *Baculentulus.*

Explanations for an eastern Asia–western-North American faunal association may be attributed to dispersal or vicariance. At present too few phylogenetic data are available to discriminate between these alternative explanations. It has generally been accepted that the Bering land connection has been the principal route for faunal dispersal from late Cretaceous (see Cox, 1974 : 86 concerning 'Asiamerica'). More recent notions have proposed that several continental plates (or terranes) have occupied what is now the Pacific Ocean and that these elements are now accreted to the margins of the Asiatic and American cratons (see discussions in Nur & Ben-Avraham, 1981 and Jones *et al.,* 1982). Thus, Asia and North America are hybrid continents and from a vicariant point of view areas of related biotic endemism within those continents should mark former plates and their associations. The numbers of plates and their former dispositions, and whether or not there were supercontinents Gondwanaland and Pacifica are hotly disputed subjects amongst geologists (see McElhinny *et al.* 1981; Batten & Schweichert, 1981; Leith, 1982; Audley-Charles, 1983; Kerr, 1983).

The distributional pattern of the aspinines within Asia and between Asia and western-North America provides general support for a vicariant explanation involving continental plate displacements. However, only more congruent cladograms of east Asiatic and western-North American biota will favour such an explanation.

Conclusion

Further progress with understanding the relationships of leuciscine and aspinine cyprinid fishes depends on:

(1) A revision of *Leuciscus.* Such will not be an easy task since apart from the strictly practical problem concerned with lack of adequate samples of Russian and eastern Asian species in Western European museums, the would-be reviser faces the taxonomic problem of dealing with what is seemingly a plesiomorphic assemblage of species.

(2) Conduct a more wide-ranging cladistic analysis of Palearctic and Nearctic non-barbelled cyprinids.

(3) Consolidation of the trans-Pacific link hypothesis through a more wide-ranging vicariance analysis of other biotas.

Acknowledgements

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