Intraspecific variation in fossil vertebrate populations: Fossil killifishes (Actinopterygii: Cyprinodontiformes) from the Oligocene of Central Europe

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ABSTRACT

A quantification of intraspecific variation in morphological traits is necessary not only as a basis for taxonomic work but also to understand a basic aspect of evolution. Comparisons among species could reveal differences in plasticity in development among them and even give clues on evolvability. Studies of this kind are rare for extinct species of vertebrates given the lack of adequate samples, but there are notable exceptions. Morphometric and meristic data were collected for three species of fossil killifish in order to quantify intraspecific variation: 67 specimens of *Prolebias rhenanus* from the Lower Oligocene of Baden-Württemberg, 40 specimens of *Pr. stenoura* from the Lower Oligocene of Puy-de-Dôme, and 141 specimens of *Paralebias cephalotes* from the Upper Oligocene of Aix-en-Provence. Nearly identical patterns of intraspecific variation exist between the two species of *Prolebias*. Fin base lengths and precaudal lengths of the vertebral column are the most variable traits in both species, followed by pterygiophore counts, then other axial length measurements and, least variable, vertebral counts. In neither species was there a significant difference in observed variation between fin and vertebral or meristic and morphometric traits. The only significant correlation shared between the two species is the positive relationship between caudal length of the vertebral column and length of the anal fin base. Precaudal length of the vertebral column is less variable in *Paralebias* than in *Prolebias*, while precaudal vertebral count is more variable, in absolute values of the coefficient of variation. Variability in elongation of precaudal vertebrae may be the underlying cause of the absence of correlation between decreased variation in precaudal length of the vertebral column and increased variation in precaudal count in *Paralebias cephalotes*. We report more similar patterns of variation among *Prolebias* congeners than between *Prolebias* and *Paralebias*, suggesting that trait variability is changing over evolutionary time in this actinopterygian lineage.

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INTRODUCTION

Macroevolutionary patterns of disparity and diversity are tied to the evolution of variation (Simpson, 1953; Mayr, 1963; Hallgrímsson and Hall, 2005; Webster, 2007, 2014; Hunt, 2007), which can be studied in geological time (Webster, 2007; De Baets et al., 2013). Examination of phenotypic variation within populations is essential for taxonomy because non-consideration of such can lead to taxon over-splitting (Hughes and Labandeira, 1995; Labandeira and Hughes, 1994). To study intraspecific variation in palaeontology, well-preserved and large samples with adequate stratigraphic information are desirable, in order to minimize sampling biases and the effect of time-averaging (Schaeffer et al., 1972; Bookstein et al., 1978; Petry, 1982; Behrensmeyer, 1982). However, comparisons between variation in extinct and extant populations of invertebrates and vertebrates show that palaeontological samples were not strongly affected by time-averaging (Bell and Legendre, 1987; MacFadden, 1989; Bush et al., 2002; Hunt, 2004a, b). Studies of variation in extinct populations or species are more common when studying invertebrates, such as trilobites (Hughes and Labandeira, 1995; Labandeira and Hughes, 1994; Webster, 2007, 2014; Hopkins, 2011), ammonoids (Hohenegger and Tatzreiter, 1992; Korn and Klug, 2007; Monnet et al., 2010; De Baets et al., 2013), and crinoids (Lane, 1963; Meyer and Ausich, 1997). Among fossil tetrapods, studies on intraspecific variation have been conducted for example for dinosaurs (Raath, 1990; Bever et al., 2011; Foth and Rauhut, 2013), ichthyosaurs (Maxwell, 2012), rodents (Renaud et al., 2006; Lazzari et al., 2010) and horses (MacFadden, 1997). Several studies on variation in extinct populations of fishes have been carried out during the last three decades, mostly concerning microstratigraphic changes in variation of meristic and morphometric characters of different body parts, or phenotypic variation as it relates to taxonomically informative characters (Bell and Haglund, 1982; Bell et al., 1985; Bell and Legendre, 1987; Cloutier, 1997; Smith, 1987; McCune, 1990, 1996; Barton and Wilson, 1999; Micklich and Klappert, 2004; Grande, 2010; Table 1).

We chose fossil populations of cyprinodontiforms as a study system in which to examine phenotypic variation in palaeontology. Cyprinodontiformes represents a speciose clade of teleosts, including extant and extinct taxa (approximately 1200 species, 125 genera) that occur in freshwater and brackish waters of Europe, Africa, and Asia (Nelson, 2006; Costa, 2012). The skeletons of many species of Oligocene and Miocene killifishes of Europe are well-preserved and articulated, present in many localities in very high numbers (Gaudant, 2013). As such, they are a good subject for studies of phenotypic variation. Fossil populations of valenciids such as *Prolebias rhenanus* Gaudant, 1981a and *Pr. stenoura* Sauvage, 1874 and of poeciliids such as *Paralebias cephalotes* (Agassiz, 1839) in particular are represented by large numbers of individuals from restricted stratigraphic and geographic intervals in France and Germany (e.g., *Pa. cephalotes*: Figure 1).

Studies of variation in extant killifishes can provide the bases for evaluation of fossils. Recent populations of closely-related species are preferred study objects for the examination of morphological differentiation within and among populations because of their occurrence in different environments and their separation by natural barriers (e.g., Hubbs and Miller, 1965; Chernoff and Hall, 1979; Parenti and Tigano, 1993; Tigano and Ferrito, 1984, 1985; Tigano et al., 1999, 2001; Doadrio et al., 2002; Ferrito et al., 2003, 2007; Garcìa et al., 2009; Costa, 2010, 2011; Reichenbacher and Reichard, 2014; Reichenbacher et al., 2007). However, the examination of variation in extant populations can provide only a snapshot of morphological variation at the tips of the phylogeny. In order to assess the manner and rate at which variation has changed through time within a single lineage, palaeontological data are essential.

The aim of this study is to quantify intraspecific variation in meristic and morphometric characters, and to examine similarities in the distribution of this variation across multiple species in a clade. We compare the degree of variation in different regions of the axial skeleton (fins versus vertebral column). We hypothesize that fin characters are more variable than vertebral characters across all species, as high levels of variability in late-forming

TABLE 1. Examples of previous studies on phenotypic variation in populations of fossil fishes.

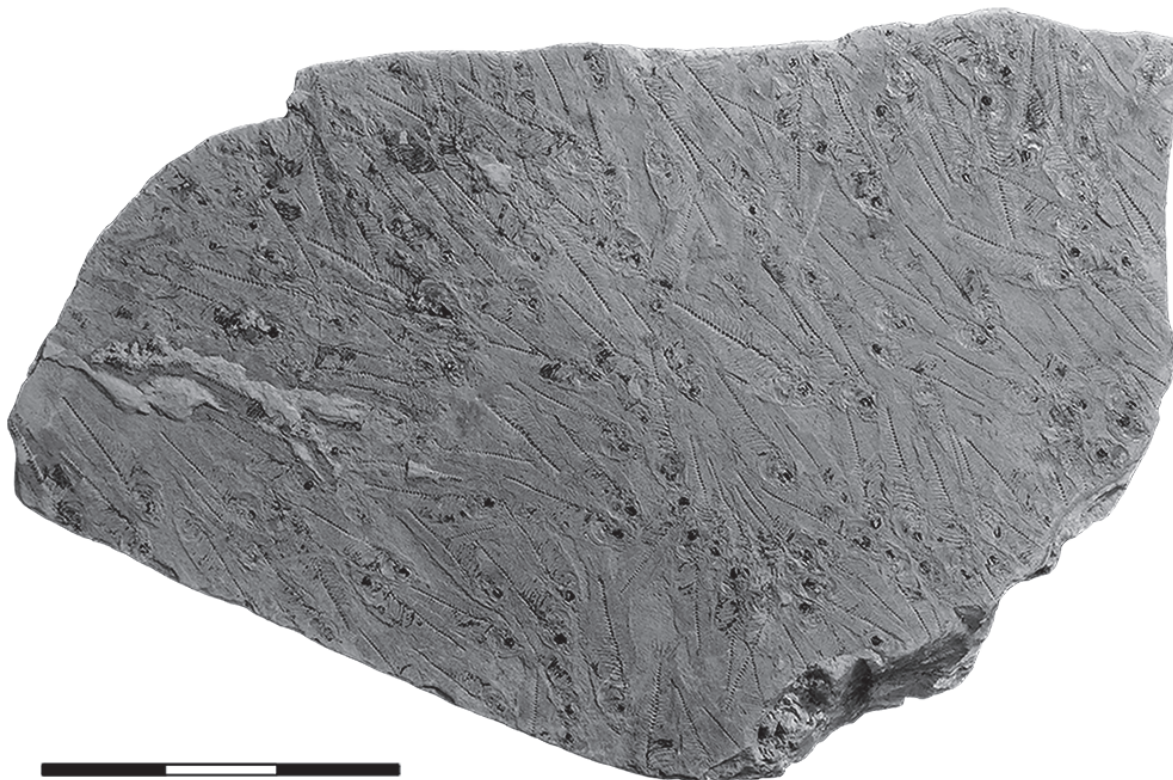| Species	Locality	Age	Environment	Objective	Characters	Source
Kenyaichthys kipkechi	Lukeino Formation, Tugen Hills, (Kenya)	late Miocene	Freshwater to brackish environment	Description of *Kenyaichthy*; Phylogenetic analyses	Various morphometric and meristic characters	Altner and Reichenbacher (2015)
Thaumaturus intermedius, Atractosteus messelensis	Messel Formation (Germany)	middle Eocene	Freshwater lake	Phenotypic variation	Meristic counts of vertebrae, rays and supports of the caudal fin; Measurements of various characters from the skull, intermuscular bones, axial skeleton and ganoin patterns	Micklich and Klappert (2004)
Lepisosteus bemisi, Atractosteus simplex, A. messelensis, A. atrox, Cuneatus cuneatus, Cuneatus wileyi	Green River Formation (USA), Messel Formation (Germany)	early–middle Eocene	Freshwater lake	Phenotypic variation	Various meristic and ratio characters from the skull, fins, and postcranial axial skeleton	Grande (2010)
Amyzon aggregatum	Horsefly beds, British Columbia (Canada)	middle Eocene	Freshwater lake	Microstratigraphic analyses of phenotypic variation	Meristic counts of vertebrae, fin rays and anal pterygiophores	Barton and Wilson (1999)
Scaumenacia curta	Escuminac Formation (Canada)	Late Devonian	Estuarine (brackish/ fluctuating salinity)	Phenotypic variation	Skull shape, dermal bone configuration	Cloutier (1997)
Semionotus	Newark Basin, New Jersey (USA)	Late Triassic – Early Jurassic	Freshwater lakes	Estimation of speciation rate	Dorsal-ridge scales, body shape	McCune (1996)
Semionotus	Towaco Formation, Newark Basin, New Jersey (USA)	Early Jurassic	Freshwater lake	Stratigraphical distribution	Dorsal-ridge scales	McCune (1990)
Gasterosteus doryssus	Truckee Formation, Nevada (USA)	Miocene	Saline lake	Temporal variation in morphology	Meristic counts of dorsal spines, predorsal pterygiophores, dorsal and anal fin rays; Measurements of pelvic structures and body length	Bell and Haglund (1982), Bell et al. (1985), Bell and Legendre (1987)
Kerocottus divaricatus K. pontifex, K. hypoceras, Kerocottus sp., *Myoxocephalus idahoensis*	Glenns Ferry Formation, Idaho (USA)	Pliocene	Freshwater Rift lake	Intralacustrine speciation	14 characters of preopercles	Smith (1987)

FIGURE 1. Photograph of a plate with *Paralebias cephalotes* (P.36131, NHM, collected from Aix-en-Provence, France). Scale bar equals 6 cm.

and peripherally located serially repeated elements have been reported in both developmental and palaeontological studies (Cloutier et al., 2010; Barton and Wilson, 1999). In addition, we examine the relationship between meristic and morphometric variation. Although logically meristic variation should result in an equal degree of morphometric variation, the relationship between these is rarely explicitly assessed. The traits we examine are relatively easy to obtain and are commonly reported in the literature. These include vertebral count (Winkler et al., 2012; Maxwell and Wilson, 2013; Aguirre et al., 2014) and median fin length (Webb, 1984), which pertain directly to fish body shape and thus ecomorphology.

MATERIALS AND METHODS

In order to obtain an estimate of variability in phenotypic features, morphometric and meristic data (characters adopted from Barton and Wilson [1999] and Hubbs and Lagler [1964]) were collected for three species of fossil killifish: *Prolebias rhenanus* Gaudant, 1981, *Pr. stenoura* Sauvage, 1874, and *Paralebias cephalotes* (Agassiz, 1839)

(Figure 2; Appendix). Each of these species of killifishes occurs at high abundance in geographically restricted areas. We sampled the following meristic characters: total vertebrae (TV), precaudal vertebrae (PV), caudal vertebrae (CV), dorsal pterygiophores (DP), and anal pterygiophores (AP). To minimise error in meristic variables, we counted meristic variables twice for each specimen, once from the anterior and once from the posterior end of the column (following Barton and Wilson, 1999). We did not include counts of fin rays as they were often badly preserved and displaced. We also collected measurement data (in mm), including standard length (SL; from the anterior part of the head to the end of the hypural plate), total length of vertebral column (TVL; from the first precaudal vertebra to the posterior end of the hypural plate), length of precaudal and caudal regions of the vertebral column (PCL and CL; from the first to the most posterior precaudal vertebrae and from the most anterior caudal vertebra to the posterior end of the hypural plate, respectively), and length of dorsal and anal fin bases (DPL and APL) (Table 2, Figures 3, 4). To avoid damage to the fossils and to obtain more accurate measurements for small

FIGURE 2. Photographs of fossil killifish species examined in this study. 1, *Prolebias rhenanus* (Ru 99, Naturhistorisches Museum Basel); 2, *Pr. stenoura* (28491 n, NHM); 3, *Paralebias cephalotes* (P.1831a, NHM). Scale bars equal 1 cm.

TABLE 2. Mean ± standard deviation and range (in parentheses) of morphometric and meristic characters for specimens of *Prolebias rhenanus*, *Pr. stenoura* and *Paralebias cephalotes*.

Character	*Prolebias rhenanus* (n = 67)	*Prolebias stenoura* (n = 40)	*Paralebias cephalotes* (n = 141)
Measurements (mm):			
Standard length	23.4 ± 3.8 (13.9–33.5)	35.9 ± 7.9 (19.0–51.0)	25.1 ± 3.0 (19–38.8)
Precaudal vertebral column length	7.6 ± 1.6 (4.0–12)	11.0 ± 3.1 (5.0–15.9)	6.9 ± 1.1 (4.9–12)
Caudal vertebral column length	9.7 ± 1.3 (5.6–12.3)	15.2 ± 3.2 (8.3–20.2)	11.4 ± 1.3 (8.1–15.5)
Dorsal fin base length	3.0 ± 0.3 (2.2–3.6)	4.5 ± 1.1 (2.3–6.9)	2.5 ± 0.5 (1.4–4.2)
Anal fin base length	3.3 ± 0.4 (2.6–4.1)	4.6 ± 1.3 (2.3–8.5)	3.4 ± 0.6 (2.1–5.6)
Meristic:			
Total vertebrae number	28.5 ± 0.7 (27–30)	30.0 ± 0.7 (29–31)	29.5 ± 1.0 (27–32)
Precaudal vertebrae number	11.9 ± 0.3 (11–12)	12.0 ± 0.3 (11–13)	10.4 ± 0.6 (10–12)
Caudal vertebrae number	16.7 ± 0.6 (16–18)	18.1 ± 0.7 (17–19)	19.2 ± 0.9 (17–21)
Dorsal pterygiophore number	10.1 ± 0.9 (8–12)	12.6 ± 1.3 (11–16)	8.6 ± 1.2 (6–11)
Anal pterygiophore number	11.0 ± 0.8 (9–13)	14.5 ± 1.2 (12–19)	12.9 ± 1.3 (10–16)

specimens, we took photos of all specimens and from them obtained measurements using the software Photoshop CS6 (Adobe Systems Incorporated, San Jose, CA, USA). We used the line tool to precisely align curves and lines to the different length parameters and later, we could easily measure the length of these shapes at the scale in the photographs. Due to incompleteness or disarticulation, not all data could be collected for every specimen.

Sixty-seven specimens of *Prolebias rhenanus* from the Lower Oligocene of the locality "Rüssgraben bei Kleinkems" (Baden-Württemberg, Germany) were included in the study (Figure 2.1). These were originally from the collection of Mathieu Mieg and are housed in the Naturhistorisches Museum of Basel, Switzerland. Mieg (1892) reported the occurrence of those fossil fishes within two thin layers consisting of "Plattiger Steinmergel" at a section at Rüssgraben bei Kleinkems. These layers are thin, not exceeding 0.15 m in thickness, and are separated by approximately 1 m of sediment (Mieg, 1892). *Prolebias rhenanus* has been hypothesized to tolerate fresh to brackish water conditions (Gaudant, 1981a) and inhabited a shallow saline lake periodically filled by freshwater from precipitation (Lutz, 1997).

We also sampled 40 specimens of *Prolebias stenoura* from the Lower Oligocene of Puy-de-Dôme, France, housed in the Natural History Museum of London (NHM) since the nineteenth century (Gaudant, 2012; Figure 2.2). The precise stratigraphic position of these specimens is unknown, but the specimens of the Croizet Collection, to which many of the specimens are attributed, were found in different lacustrine sediments around Corent (Giraud, 1902; Pécoil, 1938; Gorin, 1975). *Prolebias stenoura* occurred in a shallow meromictic lake with fresh to slightly brackish water conditions at the surface (Gaudant, 2012).

Lastly, we sampled 141 specimens of *Paralebias cephalotes* from the Upper Oligocene of Aix-en-Provence (Bouche-du-Rhône, France), housed in the Natural History Museum of London (Figure 2.3). *Paralebias cephalotes* was recovered from 12 different horizons during a modern excavation at Aix-en-Provence (Gaudant, 1978). The abundance of the species and the associated fauna fluctuated throughout the 1.6 m section. Variable species abundance and faunal composition are hypothesized to reflect changes in salinity in the lake, and *Pa. cephalotes* appears to have inhabited freshwa-

FIGURE 3. Bar charts showing frequency distribution of meristic characters for the three fossil Killifish species *Prolebias rhenanus* (yellow), *Pr. stenoura* (green) and *Paralebias cephalotes* (blue). 1, number of vertebrae; 2, number of precaudal vertebrae; 3, number of caudal vertebrae; 4, number of dorsal pterygiophores; 5, number of anal pterygiophores.

ter to slightly brackish environments (Gaudant, 1978).

Statistical analyses

Morphological measurements were log-transformed to equalize variance between different measurements, and all measurement data were corrected for size using multiple regression with the skull length as the independent variable. Size correction is necessary to exclude predictable ontogenetic changes in morphometric traits (McCoy et al., 2006). We selected multiple regression on skull length to standardize the data versus simply standardizing measurements as fractions of total or standard length because body length is not independent of length of the vertebral column, the trait of interest. As meristic traits are fixed during early ontogeny, they are independent of body size and so size-correction was not performed. To obtain an estimate of trait variability, we calculated the coefficients of variation (COV: standard devia-

tion divided by the trait mean) for each character using log-transformed and size-corrected data. We tested for overall differences in variation between fin characters and vertebral characters, and between morphometric characters and meristic characters using a Mann-Whitney U-test. Pairwise correlations between morphometric and meristic and fin and vertebral characters were examined using Spearman's rho. All analyses were performed using the statistical program PAST (Hammer et al., 2001).

RESULTS

Observed variation of characters

We obtained similar vertebral counts to those presented in Gaudant (2012) in *Prolebias stenoura*, but the range of dorsal and anal fin pterygiophore counts was much greater in our work (Table 2). In all the counts of *Problebias rhenanus* and *Paralebias cephalotes*, we found broader ranges
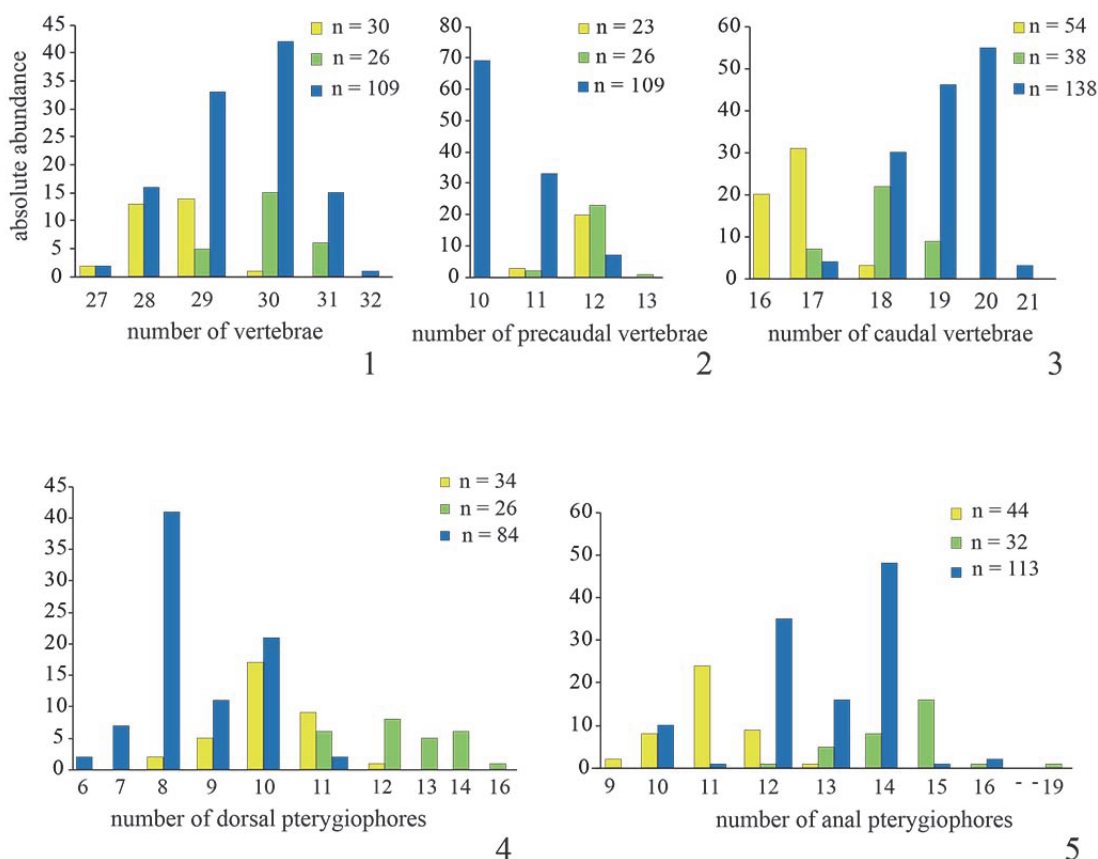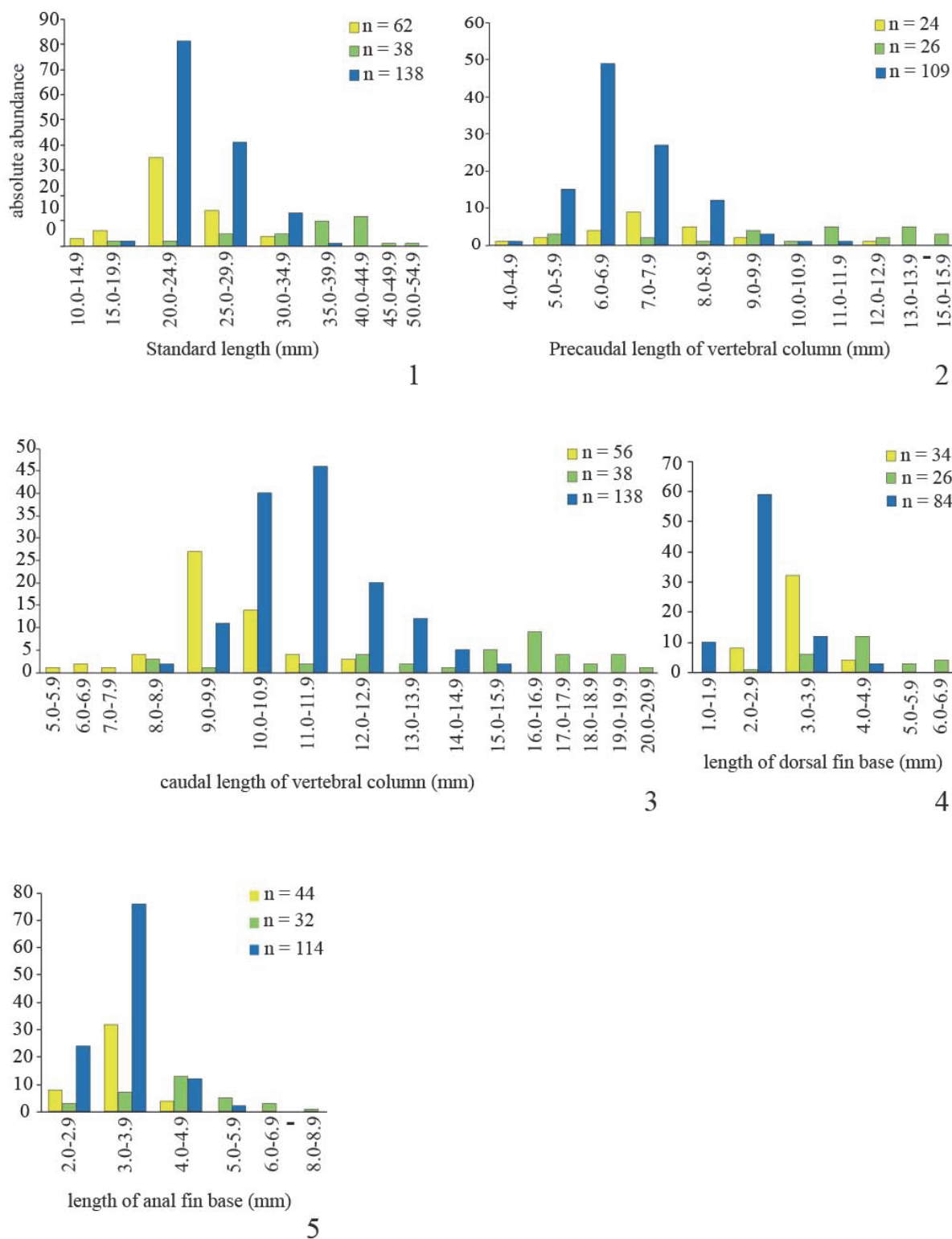
FIGURE 4. Bar charts showing frequency distribution of morphometric data (in mm) for the three fossil Killifish species *Prolebias rhenanus* (yellow), *Pr. stenoura* (green) and *Paralebias cephalotes* (blue). 1, standard length; 2, precaudal length of vertebral column; 3, caudal length of vertebral column; 4, length of dorsal fin base; 5, length of anal fin base.

TABLE 3. Coefficient of variation (COV) for morphometric and meristic characters.

Character	Coefficient of Variation		
	Prolebias rhenanus (n = 67)	*Prolebias stenoura* (n = 40)	*Paralebias cephalotes* (n = 141)
Measurements (mm):			
Standard length	5.5	6.9	3.5
Total vertebral column length	5.2	8.5	3.9
Precaudal vertebral column length	10.8	13.5	7.7
Caudal vertebral column length	6.4	9.0	4.6
Dorsal fin base length	10.8	16.8	24.0
Anal fin base length	9.8	18.4	13.8
Meristic:			
Total vertebrae number	2.4	2.2	3.4
Precaudal vertebrae number	2.9	2.9	5.9
Caudal vertebrae number	3.5	3.6	4.7
Dorsal pterygiophore number	8.8	10.3	13.5
Anal pterygiophore number	7.5	8.4	10.3

than in previous studies (Gaudant, 1981a, b, 2009). The differences in ranges are possibly attributable to different sample size.

In *Prolebias rhenanus*, lengths of the precaudal vertebral column and of the fin bases show the most variation (COV_{PCL} = 10.8, COV_{DPL} = 10.8, COV_{APL} = 9.8; Table 3). This is followed by variation in pterygiophore counts and axial length variables (COV_{DP} = 8.8, COV_{AP} = 7.5, COV_{CL} = 6.4, COV_{SL} = 5.5, COV_{TVL} = 5.2). Vertebral counts were the least variable characters in the sample; the number of caudal vertebrae was more variable than the number of precaudal vertebrae (COV_{TV} = 2.4, COV_{PCV} = 2.9, COV_{CV} = 3.5). Coefficients of variation between fin and vertebral characters are not significantly different (mean ranks 3.1 and 2.5, *P* = 0.07), nor were coefficients of variation between count and length variables (mean ranks 1.9 and 4.1, *P* = 0.12).

Based on the data presented here, length of the dorsal and anal fin bases was most variable (COV_{APL} = 18.4, COV_{DPL} = 16.8; COV_{PCL} = 13.5, see Table 3) followed by pterygiophore counts and axial length measurements (COV_{DP} = 10.3, COV_{AP} = 8.8, COV_{SL} = 6.9, COV_{TVL} = 8.5, COV_{CL} = 9.0) in *Prolebias stenoura*. Vertebral count variables showed the low coefficients of variation and with caudal counts being the most variable (COV_{TV} = 2.2, COV_{PCV} = 2.9, COV_{CV} = 3.6). Morphometric characters were not significantly more variable than meristic characters (mean ranks 4.3 and 1.7, *P* = 0.06), and differences in variation between fin and vertebral characters were not significant (mean ranks 3.0 and 2.5, *P* = 0.11).

In *Paralebias cephalotes*, lengths of the fin bases are the most variable traits, followed by pterygiophore counts (COV_{DPL} = 24.0, COV_{APL} = 13.8, COV_{DP} = 13.5 and COV_{AP} = 10.3). Measurements and counts of the precaudal vertebral column are the most variable vertebral measures (COV_{PCL} = 7.7 and COV_{PCV} = 5.9), followed by total and caudal vertebral characters (COV_{SL} = 3.5, COV_{TVL} = 3.9, COV_{CL} = 4.6, COV_{TV} = 3.4 and COV_{CV} = 4.7). Coefficients of variation of fin characters are higher than those of vertebral characters (mean ranks 3.4 and 2.1, *P* = 0.009). Mean ranks of morphometric and meristic characters do not differ significantly from each other (mean ranks 3.7 and 2.6, *P* = 0.90).

Correlation of characters

Only significant correlations are reported in the text; see Tables 4-6 for all morphometric vs. meristic and fin vs. vertebral correlations.

In *Prolebias rhenanus* the number of precaudal vertebrae is negatively correlated with anal pterygiophore count (correlation coefficient: *S* = -0.54, *P* = 0.02). Precaudal length and caudal length of

TABLE 4. Correlation matrix (correlation coefficient below the diagonal; p-values above the diagonal) for fin vs. vertebral and meristic vs. morphometric characters of *Prolebias rhenanus.* Significant correlations (α = 0.05) are highlighted in bold face fonts. Abbreviations for morphometric characters: SL, standard length; TVL, total length of vertebral column; PCL and CL, length of precaudal and caudal region of vertebral column; DPL and APL, length of dorsal and anal fin bases. Abbreviations for meristic characters: TV, total number of vertebrae; PV and CV, number of precaudal and caudal vertebrae; DP and AP, number of dorsal and anal pterygiophores.

	SL	DPL	APL	TVL	PCL	CL	DP	AP	TV	PCV	CV
SL							0.949	0.195	0.120	0.478	0.477
DPL				**0.0001**	**0.0043**	**0.0358**	**0.0003**	0.783	0.407	0.596	0.343
APL				**7.53×10-5**	**0.0169**	**9.18×10-7**	0.920	0.641	0.886	0.724	0.986
TVL		0.466	0.481				0.949	0.190	0.0914	0.424	0.589
PCL		0.358	0.303				0.604	0.172	0.130	0.424	0.391
CL		0.267	0.577				0.579	0.480	0.325	0.374	0.22
DP	-0.0115	0.579	-0.0179	-0.0115	-0.0923	-0.0986			0.052	0.9324	0.234
AP	0.199	-0.0428	0.0724	0.201	0.210	-0.109			0.358	**0.0238**	0.0682
TV	-0.290	0.157	-0.0273	-0.314	-0.283	-0.186	0.453	-0.211			
PCV	-0.156	0.117	-0.0779	-0.175	-0.175	0.195	0.024	-0.545			
CV	-0.0988	0.132	-0.0024	-0.0751	-0.119	-0.170	0.228	-0.295			

TABLE 5. Correlation matrix (correlation coefficient below the diagonal; p-values above the diagonal) for fin vs. vertebral and meristic vs. morphometric characters of *Prolebias stenoura.* Significant correlations (α = 0.05) are highlighted in bold face fonts. Abbreviations are the same as in Table 4.

	SL	DPL	APL	TVL	PCL	CL	DP	AP	TV	PCV	CV
SL							0.629	0.907	0.580	0.219	0.774
DPL				0.553	0.899	0.628	0.103	0.366	0.185	0.621	0.252
APL				0.112	0.451	**0.0444**	0.879	**0.0138**	0.299	0.0758	0.0868
TVL		0.099	0.262				0.629	0.907	0.580	0.219	0.774
PCL		0.0212	0.126				0.292	0.584	0.770	0.396	0.737
CL		0.0811	0.328				0.862	0.558	0.915	0.220	0.681
DP	-0.0994	0.327	0.0313	-0.0994	-0.215	-0.0342			0.746	0.251	0.667
AP	0.0214	-0.166	0.431	0.0214	-0.101	0.108			0.344	0.106	0.0762
TV	-0.114	-0.268	0.212	-0.114	-0.0604	0.0219	-0.0849	0.212			
PCV	-0.250	-0.102	-0.354	-0.250	-0.174	-0.249	0.292	-0.354			
CV	0.0482	-0.190	0.282	0.0482	0.0563	0.0689	-0.0885	0.318			

the vertebral column are both positively correlated with length of the fin bases (PCL: $S = 0.36$, $P = 0.004$; $S = 0.3$, $P = 0.01$; CL: $S = 0.27$, $P = 0.03$; $S = 0.58$, $P = 9.18×10^{-7}$). The relationship between length of the dorsal fin base and number of dorsal pterygiophores is significant and positive ($S = 0.58$, $P = 0.0003$) (Table 4).

In *Prolebias stenoura*, caudal length of the vertebral column is positively correlated with length of the anal fin base ($S = 0.32$; $P = 0.04$). The relationship between the base of the anal fin and the number of anal pterygiophores is significant and positive ($S = 0.43$, $P = 0.01$) (Table 5).

In *Paralebias cephalotes*, fin base lengths are positively correlated with all vertebral length traits. Caudal length is negatively correlated with the number of precaudal vertebrae ($S = -0.49$, $P = 0.04$), but positively correlated with number of caudal vertebrae ($S = 0.25$, $P = 0.002$). The length of the dorsal fin base is significantly correlated with the number of dorsal pterygiophores ($S = 0.46$, p-values = $9.44×10^{-6}$), and the length of the anal fin base is significantly correlated with the number of

TABLE 6. Correlation matrix (correlation coefficient below the diagonal; p-values above the diagonal) for fin vs. vertebral and meristic vs. morphometric characters of *Paralebias cephalotes.* Significant correlations (α = 0.05) are highlighted in bold face fonts. Abbreviations are the same as in Table 4.

	SL	DPL	APL	TVL	PCL	CL	DP	AP	PCV	CV	TV
SL							0.458	0.352	0.355	0.323	0.749
DPL				**0.0001**	**0.0165**	**1.04×10-5**	**9.44×10-6**	0.557	0.603	0.322	0.582
APL				**8.92×10-8**	**0.0003**	**6.92×10-9**	0.185	**7.02×10-4**	0.295	0.377	0.909
TVL		0.322	0.436				0.394	0.339	0.556	0.192	0.430
PCL		0.204	0.302				0.915	0.395	0.204	0.344	0.934
CL		0.366	0.468				0.152	0.418	**0.0444**	**0.0023**	0.145
DP	0.0820	0.463	0.146	0.0943	0.0118	0.158			0.735	0.651	0.986
AP	-0.0884	0.0558	0.314	-0.0907	-0.0807	-0.0770			0.474	0.849	0.584
PCV	-0.0895	-0.0503	-0.101	-0.0570	0.123	-0.193	-0.0421	-0.0765			
CV	0.0847	0.0850	0.0759	0.112	-0.0812	0.258	0.0501	0.0181			
TV	0.0310	0.0533	0.0111	0.0763	-0.008	0.141	-0.0022	-0.0584			

anal pterygiophores (S = 0.31, P = 7.02×10^{-4}) (Table 6).

DISCUSSION

Nearly identical patterns of intraspecific variation exist between the two species of *Prolebias*. Length of the fin base and of precaudal parts of the vertebral column are the most variable traits in both species, followed by pterygiophore counts, then other axial length measurements and, least variable, vertebral counts. The magnitude of the observed variation for most traits, including measurements and pterygiophores counts, is greater in *Pr. stenoura*, but the coefficient of variation for the vertebral counts are identical in both species. In neither species was there a significant difference in observed variation between fin and vertebral or meristic and morphometric traits. In the samples of both species, there is a positive relationship between caudal length of the vertebral column and length of the anal fin base. Interestingly, although *Pr. stenoura* shows relatively greater amounts of variation for most traits, this variation appears to be stochastically distributed: for the trait combinations tested, *Pr. rhenanus* exhibits more and stronger covarying trait relationships.

The pattern of variation observed in *Paralebias cephalotes* is similar to *Prolebias*, with one major exception: precaudal length (COV$_{PCL}$ = 7.7) is less variable in *Paralebias* while precaudal vertebral count (COV$_{PCL}$ = 5.9) is more variable. However, as it was the case in *Prolebias*, this variation appears to be randomly distributed: precaudal length and the number of precaudal vertebrae are not significantly correlated, suggesting that the decrease in variation observed in the first and the increase in variation observed in the second are not due to trait integration. In addition, a significant difference in variability was detected between fin and vertebral characters, with vertebral characters being less variable in *Pa. cephalotes*. The relative amount of variation observed was slightly, but not dramatically greater in *Pa. cephalotes* (mean ranks 3.7 and 2.6, P = 0.90) than in *Pr. stenoura* (mean ranks 3.0 and 2.5, P = 0.11), and may be attributed to larger sample sizes in the former.

Decreased variation in precaudal length of the vertebral column and increased variation in precaudal count in *Paralebias cephalotes* in the absence of any correlation between the two traits suggests an underlying cause: variability in elongation of precaudal vertebrae. This pattern clearly does not extend into the caudal region, where a significant relationship exists between caudal length and number of caudal vertebrae, as reported in an extensive and phylogenetically broad examination of bony fishes species (Lindsey, 1975). Elongate fishes extend the vertebral column either through elongation of the vertebral centra or through addition of vertebrae (Ward and Mehta, 2010), and our results imply that variation in both vertebral number and vertebral length may be present in populations.

In *Prolebias* spp. caudal vertebral counts (COV$_{CV}$ = 3.5 for *Pr. rhenanus* and 3.6 for *Pr. stenoura*, respectively) are significantly more variable than precaudal counts (COV$_{PCV}$ = 2.9 for both species). The pre-ural caudal region of the vertebral

column in fishes is hypothesized to be more variable than the precaudal region, as segmentation proceeds from anterior to posterior (Itazawa, 1963; Nagiec, 1977; Lindsey, 1988; Grande and Bemis, 1998; Barton and Wilson, 1999; Aguirre et al., 2014), and most actinopterygians add vertebrae to the caudal region preferentially (Ward and Mehta, 2014), suggesting increased variability in this region. However, this is not a universal rule: some actinopterygians do add vertebrae preferentially to the abdominal region (Mehta et al., 2010; Maxwell and Wilson, 2013), and this may result in increased variability in abdominal counts within species. Sexual dimorphism may also increase observed variation in abdominal vertebral counts preferentially relative to caudal counts due to selection for increased abdominal volume in females (Lindsey, 1975).

Intraspecific variation in vertebral counts is correlated with a multitude of factors in teleosts, including life history (McDowall, 2003), sex (Aguirre et al., 2014; Lindsey, 1975), habitat (Shikano and Merilä, 2011), and temperature/latitude/altitude (Barriga et al., 2013; Baumann et al., 2012; Hice et al., 2012; McDowall, 2003; Yamahira et al., 2006; Yamahira and Nishida, 2009). Heritability of vertebral numbers is high, but phenotypic plasticity is well documented (Lindsey, 1988; Yamahira and Nishida, 2009). Differences in sample size, multiyear sampling effects, salinity, and other habitat characteristics may influence the absolute amount of variation observed, as has been reported in other teleosts (e.g., McDowall, 2003; Shikano and Merilä, 2011), including killifishes (Maltagliati et al., 2003). *Prolebias rhenanus* and *Paralebias cephalotes* inhabited brackish waters with fluctuating salinity content, whereas *Pr. stenoura* inhabited freshwater lakes. As the pattern of variation between *Problebias* spp., which lived in different water conditions, is similar, differences in salinity do not seem to have affected such variation. Moreover, the number of precaudal vertebrae in fossil killifishes was difficult to observe, since the most anterior vertebrae are often badly preserved or covered by the skull (Gaudant, 1981a), and thus measurement error cannot be eliminated as a source of increased variation.

Variability between fin and vertebral characters is similar in *Prolebias* spp. (*Prolebias rhenanus*: mean ranks 3.0 and 2.5, *P* = 0.11; *Pr. stenoura*: mean ranks 3.0 and 2.5, *P* = 0.11), but *Paralebias cephalotes* (mean ranks 3.7 and 2.6, *P* = 0.90) shows greater variability in characters pertaining to the median fins. However, even in *Pro-*

lebias spp. traits pertaining to the dorsal and anal fins are extremely variable (*Prolebias rhenanus*: $COV_{APL, AP, DPL, DP}$ = 9.8, 7.5, 10.8, 8.8; *Pr. stenoura*: $COV_{APL, AP, DPL, DP}$ = 18.4, 8.4, 16.8, 10.3). Although descriptive statistics pertaining to morphological variation (i.e., mean, standard deviation) are rarely presented for extant cyprinodontiforms, those few data that are available are consistent with our observations. For instance, the COV_{TV} and the COV of axial length measurements are less than those of both dorsal and anal fin ray counts in males of the extant poeciliid *Gambusia quadruncus* (Langerhans et al., 2012); females appear to be more variable than males but all COV values fall into the range reported in our fossil samples (e.g., $COV_{(TV♀)}$ = 2.4%). In three goodeid species belonging to *Xenoophorus*, length measurements pertaining to vertebral regions also had on average lower coefficients of variation than the lengths of the fin bases, with the length of the anal fin base showing the highest COV and the length of the axial skeleton anterior to the dorsal fin showing the least variation in all species. Count data were not available. As in *Gambusia*, females showed overall slightly higher amounts of variation than males (Fitzsimons, 1979).

Variation in vertebral counts should theoretically be lower than in pterygiophore (proximal radial) counts in fishes, based on a more terminal position of the latter in the developmental sequence (both in terms of patterning and ossification) resulting in an increased number of ways in which variation may be introduced (Lindsey, 1988). This effect may be amplified in fossil fishes, since pterygiophores ossify relatively late in ontogeny (e.g., Bird and Mabee, 2003; Grünbaum et al., 2012) and thus may not be preserved in smaller specimens even when present. Higher variability in pterygiophore counts than vertebral counts is supported in a species of catastomid (Barton and Wilson, 1999). Studies on variation in fishes have reported that fin traits are more variable than vertebral ones in general (Cloutier et al., 2010; Barton and Wilson, 1999; MacGregor and MacCrimmon, 1977). Median fins rely on the same positioning cues as the vertebral column early in development (Freitas et al., 2006) and later in development articulate with the neural and haemal spines (Figure 2) (Bird and Mabee, 2003). This suggests that, to a certain degree, the two sets of traits should be correlated: as the vertebrae grow longer, the bases of the fins are also constrained to become longer, and indeed this is what is observed in our studied samples, with all species showing a positive correlation

between the lengths of at least one of the fin bases and the vertebral column. However, the lengths of the fin bases are also related to the number of pterygiophores, and this appears to be the underlying cause of observed variation in fin characters. Pterygiophores ossify late in development (Fischer-Rousseau et al., 2009; Cloutier et al., 2010; Grünbaum et al., 2012), and environmentally induced plasticity is observed in their timing of ossification (Cloutier et al., 2010; Grünbaum et al., 2012) so it is uncertain whether variable ossification rather than meristic variability is promoting variation in fin characters.

In conclusion, our data suggest similarities in patterns of variation among closely related species, with possible divergence of trait variability between 'families' (Poeciliidae - *Paralebias* vs. Valenciidae - *Prolebias*: Costa, 2012; Gaudant, 2013). More thorough sampling within Cyprinodontiformes is needed to evaluate the time-scales over which such shifts occur. Divergence in patterns of trait covariance have previously been reported over a range of time and spatial scales (population: Game and Caley, 2006; stratigraphic: Maxwell and Dececchi, 2013; phylogenetic: Goswami et al., 2014), and variability in the amount of morphological variation present has been shown in a general way between populations (Game and Caley, 2006). Our results suggest that not only can the variance-covariance matrix be restructured, and different amounts of absolute variation be present (Wilson, 2013), but the variability of specific traits also changes over evolutionary time. The ~10% absolute variation in vertebral numbers among individuals we found may have influenced locomotory performance in the populations studied (Brainerd and Patek, 1998; Spouge and Larkin, 1979), although the relationship between vertebral numbers and locomotory performance is complex.

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APPENDIX

Meristic and morphometric data collected for this study.

Species	Specimen	Standard length	Dorsal fin base length	Anal fin base length	Total vertebral length	Precaudal length	Caudal length	Dorsal pterygiophores number	Anal pterygiophores number	Total vertebrae number	Precaudal vertebrae number	Caudal vertebrae number	Skull length
Prolebias rhenanus	Ru99	29.2	3.5	3.4	19.8	9.1	10.7	10	11	29	12	17	9.4
	Ru91	28	3.5	3.2	?	?	10.4	11	12	?	?	16	?
	Ru24	26.8	?	?	18.8	8.8	10	?	?	28	11	17	8
	Ru8	13.9	?	?	?	?	5.6	?	?	?	?	16	?
	Ru1	16.9	?	2.9	13.5	5.6	7.9	?	11	28	12	16	3.4
	Ru61	23.1	2.8	3.3	16.4	7.4	9	9	11	30	12	18	6.7
	Ru62	24.9	?	2.9	?	?	9.5	?	12	?	?	17	?
	Ru63	27.8	?	?	?	?	11.1	?	?	?	?	17	?
	Ru64	23.2	2.9	3.6	17.1	?	?	10	12	28	?	?	6.1
	Ru65	23.5	3	4.1	16.8	7	9.8	11	10	29	12	17	6.7
	Ru67	29.5	3.6	3.7	20.3	9.8	10.5	11	12	28	11	17	9.2
	Ru70	23.3	?	?	17.4	?	?	?	?	27	?	?	5.9
	Ru73	30.5	?	3.7	?	?	12.2	?	11	?	?	16	?
	Ru80	25.6	3.3	3.1	18.4	8.8	9.6	11	13	29	12	17	7.2
	Ru82	21.9	2.7	2.9	15.5	6	9.5	10	9	28	12	16	6.4
	Ru95	23	3	3.1	17.6	8.2	9.4	10	10	29	12	17	5.4
	Ru115	22.5	3.2	4.1	?	?	9.5	11	12	?	?	16	?
	Ru87	22.7	?	2.8	?	?	9.5	?	11	?	?	16	?
	Ru89	22.9	2.9	3.5	?	?	9.6	10	12	?	?	16	?
	Ru90	19.2	?	?	?	?	8.6	?	?	?	?	17	?
	Ru92	31.6	?	4	?	?	12.3	?	10	?	?	17	?
	Ru96	20	?	?	?	?	8.6	?	?	?	?	16	?
	Ru98	23.4	3	3.1	?	?	9.8	12	12	?	?	17	?
	Ru100	19.8	2.4	3.5	15.6	6.6	9	9	12	27	11	16	4.2
	Ru102	24.2	3.4	3.3	16.9	7	9.9	11	11	29	12	17	7.3
	Ru107	25.5	?	3.1	?	?	10.9	?	11	?	?	17	?
	Ru111	14.3	2.3	?	10.1	4	6.1	10	?	29	12	17	4.2
	Ru113	23.3	3.5	3.7	18.3	7.7	10.6	11	10	29	12	17	5
	Ru116	27.1	?	3.3	?	?	10.7	?	11	?	?	16	?

Species	Specimen	Standard length	Dorsal fin base length	Anal fin base length	Total vertebral length	Precaudal length	Caudal length	Dorsal pterygiophores number	Anal pterygiophores number	Total vertebrae number	Precaudal vertebrae number	Caudal vertebrae number	Skull length
	DSC4221	25.9	?	?	18	7.9	10.1	?	?	?	?	16	7.9
	Ru74	24.9	?	3.2	18.9	8.5	10.4	?	11	28	12	16	6
	Ru173	22.8	2.7	3.4	?	?	9.6	10	11	?	?	17	?
	Ru3	25.2	3.3	3.9	18.3	7.5	10.8	11	11	29	12	17	6.9
	Ru4	23.1	2.9	3.2	?	?	9.8	10	10	?	?	17	?
	Ru7	14.1	?	?	?	?	6.2	?	?	?	?	17	?
	Ru11	22.4	?	?	14.6	5.6	9	?	?	29	12	17	7.8
	Ru12	19	2.2	3.1	?	?	8.5	10	11	?	?	18	?
	Ru16	26	2.9	3.1	?	?	10.2	10	11	?	?	17	?
	Ru13	22	2.8	3.8	16.6	6.9	9.7	8	11	28	12	16	5.4
	Ru17	23.9	3.1	3.9	17.4	6.9	10.5	10	11	29	12	17	6.5
	Ru18	22.2	?	?	17.6	8	9.6	?	?	28	12	16	4.6
	Ru19	22.1	2.9	3.1	?	?	9.8	9	11	28	?	?	?
	Ru25	22.6	2.8	2.6	?	?	?	10	11	?	?	?	?
	Ru27	21.6	?	?	?	?	9.6	?	?	?	?	17	?
	Ru30	26.9	?	3.2	18.5	7.5	11	?	11	29	12	17	8.4
	Ru34	22.9	3	3.2	15	?	?	10	11	28	?	?	7.9
	Ru46	23.9	3.1	2.7	?	?	11.2	10	9	?	?	18	?
	Ru53	25.1	3.3	?	?	?	10	11	?	?	?	17	?
	Ru56	18.9	?	?	?	?	9.1	?	?	?	?	17	?
	Ru31	23.3	?	2.9	?	?	9.9	?	11	?	?	16	?
	Ru33	23.9	?	?	17.1	?	?	?	?	29	?	?	6.8
	Ru26	23.9	?	?	17.7	?	?	?	?	28	?	?	6.2
	Ru23	19.9	2.5	3	?	?	8.5	10	12	?	?	16	?
	Ru20	21.1	2.7	3.5	?	?	9.5	8	11	?	?	16	?
	Ru66	33.5	3.1	4	24	12	12	9	11	28	12	16	9.5
	DSC4282=1	23.1	?	?	17	7.5	9.5	?	?	29	12	17	6.1
	DSC4283	20.9	3	3.5	?	?	9.1	10	11	?	?	16	?
	DSC4284	22.1	?	3	?	?	9.9	?	10	?	?	17	?
	DSC4293	30	3	3.9	?	?	11.2	9	10	28	?	?	?
	DSC4295=2	20.4	?	?	16.1	7	9.1	?	?	29	12	17	4.3

Species	Specimen	Standard length	Dorsal fin base length	Anal fin base length	Total vertebral length	Precaudal length	Caudal length	Dorsal pterygiophores number	Anal pterygiophores number	Total vertebrae number	Precaudal vertebrae number	Caudal vertebrae number	Skull length
	DSC4299=4	25.6	?	2.9	?	?	10	?	10	?	?	17	?
	DSC4294	22.4	3.1	3.2	?	?	9.8	10	11	?	?	17	?
Prolebias stenoura	28491n	39.8	5.7	6.5	32.6	13.6	19	12	15	30	12	18	7.2
	28491	35.3	4	5.4	26.6	10.1	16.5	13	15	31	12	19	8.7
	28491k	42	?	?	32.8	15.9	16.9	?	?	30	12	18	9.2
	1908	34.1	6.8	4.4	25.7	9	16.7	16	15	30	12	18	8.4
	P57078	51	6.9	8.5	35.7	15.5	20.2	11	15	30	11	19	15.3
	P57069	40.5	5.2	5.3	?	?	16.4	14	15	?	?	19	?
	P57068	27	3.2	4.1	20.4	7.5	12.9	12	15	30	12	18	6.6
	P57073	36	4	4.1	26.7	11	15.7	11	14	30	12	18	9.3
	P57063	27.1	3.5	3.4	19.6	7.9	11.7	12	14	30	12	18	7.5
	P57053	40.5	?	5.1	29.1	11.5	17.6	?	15	29	12	17	11.4
	P57057	33.3	3.9	3.5	?	?	14.1	13	15	?	?	18	?
	P57059	41.4	4.3	4	31.4	12.8	18.6	11	13	31	12	19	10
	P57057b	42.8	3.7	5.4	31.3	13.1	18.2	11	15	31	12	19	11.5
	P57058	36.9	4.4	4.8	?	?	16.7	13	15	?	?	18	?
	P1832a	44.4	6.2	6.4	31.2	12	19.2	14	16	31	12	19	13.2
	P1832	45	?	4.9	31	13.5	17.5	?	15	30	12	18	14
	P1832b	41.3	3.8	4.6	?	?	16.9	12	15	?	?	17	?
	21416	29.5	?	3.9	21.2	8.4	12.8	?	14	31	12	19	8.3
	28491m	38.5	4	4.6	27.7	11.9	15.8	13	19	30	12	18	10.8
	28491.1	37.1	4.1	3.8	?	?	15.1	12	15	?	?	18	?
	28491.2	39.2	4.2	4.9	?	?	15.7	12	13	?	?	17	?
	28491c	29.3	3.7	3.7	?	?	12	14	15	?	?	18	?
	28491h	31.1	?	2.3	22	9.2	12.8	?	13	30	13	17	9.1
	28491g	26.1	?	?	?	?	11	?	?	?	?	19	?
	28496.1	39.1	6.7	5.3	28	11.6	16.4	13	13	29	12	17	11.1
	28496.3	33.2	?	3.9	25.5	11.7	13.8	?	14	29	12	17	7.7
	28496.4	43	?	?	33.7	13.8	19.9	?	?	29	11	18	9.3
	28491l	31.5	4	3.7	22.8	9.6	13.2	14	14	30	12	18	8.7
	28491o	40	4.9	?	?	?	17.2	14	?	?	?	18	?

Species	Specimen	Standard length	Dorsal fin base length	Anal fin base length	Total vertebral length	Precaudal length	Caudal length	Dorsal pterygiophores number	Anal pterygiophores number	Total vertebrae number	Precaudal vertebrae number	Caudal vertebrae number	Skull length
	28491p	19.8	2.3	?	14	5.7	8.3	12	?	31	12	19	5.8
	28491r	20.9	?	2.6	?	?	9	?	13	?	?	18	?
	28491q	21.8	?	2.6	14.3	5.7	8.6	?	14	29	12	17	7.5
	28491s	42	4.8	4.3	29.7	13	16.7	12	14	30	12	18	12.3
	28491u	19	?	?	13.5	5	8.5	?	?	30	12	18	5.5
	28491v	49.5	?	6.5	?	?	19.2	?	15	?	?	18	?
	28491t	42.9	5	4.6	33.1	15.9	17.2	11	14	30	12	18	9.8
	P3851	35.6	4	4.3	24.9	9.8	15.1	11	15	30	12	18	10.7
	21417	37.5	4.4	4.6	?	?	16	14	12	?	?	18	?
Paralebias cephalotes	1831a	24.9	2.1	4.9	?	?	11.2	7	14	?	?	18	?
	43438	23.6	2.6	2.1	16.7	6.4	10.3	9	13	29	10	19	6.9
	21397	24.3	?	3.2	17.9	7.6	10.3	?	10	30	12	18	6.4
	21396.1	24	2.2	2.8	17.6	6.6	11	9	12	31	12	19	6.4
	21396.2	24.9	?	3.7	17.1	6	11.1	?	16	29	10	19	7.8
	P.1831.1	31.2	3.1	3.5	23.4	8.5	14.9	9	12	30	10	20	7.8
	P.1831.2	22.8	2.2	3.2	16.8	6.8	10	10	13	31	12	19	6
	P.1831.3	26.7	?	3.9	19.5	6.5	13	?	12	30	10	20	7.2
	P.1831.4	28.1	2.6	3.9	20.6	6.9	13.7	8	13	30	10	20	7.5
	P.1831.5	26.9	2	3.5	18.6	6.1	12.5	7	14	30	10	20	8.3
	P.1831.8	22	2.9	2.8	?	?	9.5	9	14	?	?	19	?
	P.1831.9	20.8	?	2.6	?	?	9.6	?	12	?	?	19	?
	P.1831.12	23.2	1.9	2.7	?	?	10.7	7	13	?	?	20	?
	P.1831.13	23.5	?	2.9	?	?	11.7	?	13	?	?	21	?
	P.1831.14	23.3	?	2.5	18.2	7.1	11.1	?	11	32	11	21	5.1
	P.1831.16	22.2	2.1	3.9	17.5	5.8	11.7	9	14	30	10	20	4.7
	20071.1	22	2.7	3	16.4	5.9	10.5	9	?	30	11	19	5.6
	20071.2	23.7	?	2.9	17.4	6	11.4	?	10	30	10	20	6.3
	20071.6	21.2	?	?	?	?	10.3	?	?	?	?	20	?
	20071.10	23.7	?	2.7	16.8	5.8	11	?	12	29	10	19	6.9
	20071.11	22.5	?	?	16.3	6.3	10	?	?	28	10	18	6.2
	20071.12	28.9	3	3.7	21.3	8.1	13.2	10	13	30	11	19	7.6

Species	Specimen	Standard length	Dorsal fin base length	Anal fin base length	Total vertebral length	Precaudal length	Caudal length	Dorsal pterygiophores number	Anal pterygiophores number	Total vertebrae number	Precaudal vertebrae number	Caudal vertebrae number	Skull length
	20071.14	21	?	3.3	17.1	5.9	11.2	?	13	30	10	20	3.9
	20071.15	22.7	2.1	3.4	?	?	10.8	8	14	?	?	20	?
	20071.17	23.9	?	3	16.9	6.3	10.6	?	12	28	10	18	7
	20071.19	23.4	?	3.5	17.3	7.6	9.7	?	14	29	12	17	6.1
	20071.23	29.6	3	4.1	20.5	7.7	12.8	9	14	29	10	19	9.1
	20071.30	32.5	?	4.9	?	?	15.5	?	12	?	?	20	?
	20071.29	23.1	2.2	3	17.8	7.5	10.3	9	12	28	11	17	5.3
	20071.28	22.8	?	?	15.9	5.8	10.1	?	?	29	10	19	6.9
	36131.1	28.8	2.3	3.9	21.7	8.6	13.1	8	14	29	11	18	7.1
	36131a	25.1	2.1	3.7	?	?	11.8	8	14	?	?	19	?
	36131.2	24.7	2	3.4	?	?	12	8	13	?	?	19	?
	36131.5	20.9	?	?	15.4	4.9	10.5	?	?	30	11	19	5.5
	36131.6	23.2	2	3.2	16.4	5.7	10.7	8	13	29	10	19	6.8
	36131.8	26.4	?	2.9	19.7	7.7	12	?	12	29	11	18	6.7
	36131.9	24.9	1.9	2.8	23.6	12	11.6	8	10	28	10	18	1.3
	36131.10	25	?	?	17.8	7.1	10.7	?	?	28	10	18	7.2
	36131.11	23.6	?	?	17.1	5.6	11.5	?	?	30	10	20	6.5
	36131.12	26.5	4	2.7	19.2	6.7	12.5	9	12	30	10	20	7.3
	36131.13	21.5	2.3	3	16.4	6	10.4	10	14	31	11	20	5.1
	36131.14	23.8	?	3.6	16.6	6.2	10.4	?	14	30	10	20	7.2
	36131.17	25	?	3	?	?	11.1	?	14	?	?	20	?
	36131.20	23.9	2.1	3.3	18.2	7	11.2	8	14	28	10	18	5.7
	36131.23	23.9	?	2.9	16.7	5.9	10.8	?	12	28	10	18	7.2
	36131.25	25.9	2.4	3.3	18.2	6.7	11.5	8	12	29	10	18	7.7
	36131.26	23.9	?	4	?	?	12.1	?	14	?	?	20	?
	36131.27	24.2	1.7	2.4	18.6	7.8	10.8	8	12	29	10	19	5.6
	36131.29	26.5	?	3.6	19.9	7.3	12.6	?	10	28	10	18	6.6
	36131.28	24	?	2.5	16.2	6.4	9.8	?	14	27	10	17	7.8
	36131.31	24.9	2	3.1	17	6.3	10.7	7	14	29	11	18	7.9
	36131.34	25.4	?	?	19.4	7.9	11.5	?	?	28	10	18	6
	36131.37	31.2	?	?	21.5	7.6	13.9	?	?	28	10	18	9.7
	36131.41	25.3	2	3.8	19.3	6.8	12.5	8	14	30	10	20	6

Species	Specimen	Standard length	Dorsal fin base length	Anal fin base length	Total vertebral length	Precaudal length	Caudal length	Dorsal pterygiophores number	Anal pterygiophores number	Total vertebrae number	Precaudal vertebrae number	Caudal vertebrae number	Skull length
	21396.1	25.4	2.6	3.7	18	6.2	11.8	8	14	29	10	19	7.4
	21396.2	30.2	2.7	4.5	21.3	7.4	13.9	10	13	30	10	20	8.9
	21396.3	22.8	?	3.2	15.8	6.2	9.6	?	14	30	11	19	7
	21396.4	31.1	3.2	3.9	21.9	8.9	13	10	14	28	10	18	9.2
	21396.5	38.8	?	3.7	20.5	8.2	12.3	?	14	30	10	20	18.3
	21396.6	23.6	3.1	4	16.6	6.5	10.1	8	14	29	10	19	7
	21396.7	23.1	2	3.3	17	6.5	10.5	8	14	30	10	20	6.1
	21396.8	25.5	?	?	18.6	8	10.6	?	?	28	10	18	6.9
	21396.10	21	2.8	3.4	18.6	6.8	11.8	12	14	28	10	18	2.4
	21396.14	23.4	?	3.7	16.8	6.1	10.7	?	14	29	10	19	6.6
	21396.15	23.5	?	3.7	17.3	6.3	11	?	14	29	10	19	6.2
	21396.16	23.7	1.9	2.9	?	?	11.3	7	12	?	?	20	?
	21396.17	27.8	2.9	3.8	19.9	6.9	13	10	13	30	10	20	7.9
	P.4266.1	22.1	?	?	?	?	9.8	?	?	?	?	18	?
	P.4266.2	23.8	2.5	?	17.2	6.7	10.5	8	?	31	11	20	6.6
	P.4266.3	25.3	?	3.3	18.4	6.7	11.7	?	14	30	10	20	6.9
	P.4266.5	19	?	?	13.5	5.4	8.1	?	?	29	11	18	5.5
	P.4266.6	27.2	2.1	3.7	21	8.5	12.5	8	14	31	12	19	6.2
	P.4266.11	23.9	2.2	3.3	17.2	5.9	11.3	10	12	30	10	20	6.7
	P.4266.12	24.5	2.5	3.6	?	?	11.5	9	12	?	?	19	?
	P.4266.13	24.5	2	3	17.4	6.8	10.6	8	10	31	11	20	7.1
	P.4266.15	21.5	2.6	2.9	16.1	6.2	9.9	10	12	30	11	19	5.4
	P.4266.16	21.9	?	2.7	15.5	5.5	10	?	14	30	10	20	6.4
	P.4266.17	23.1	?	3	?	?	11	?	12	?	?	21	?
	P.4266.18	24.2	2.5	3.7	17.3	6.6	10.7	8	14	29	10	19	6.9
	P.4266.19	26.8	2.5	3.2	?	?	12.5	8	12	?	?	19	?
	P.4266.20	22.3	2	3.1	16.6	6.7	9.9	8	14	27	10	17	5.7
	P.4266.21	32	3.1	4.5	23.5	10	13.5	8	14	29	10	19	8.5
	P.4266.22	25.2	2.9	3.5	18.7	6.2	12.5	12	12	30	10	20	6.5
	P.4266.24	19.3	1.4	2.9	14.5	5.8	8.7	7	12	30	10	20	4.8
	P.4266.25	30.5	3.2	4.5	23.7	8.7	15	10	12	30	10	20	6.8
	P.4266.26	24	?	?	17.8	6.8	11	?	?	29	11	18	6.2

Species	Specimen	Standard length	Dorsal fin base length	Anal fin base length	Total vertebral length	Precaudal length	Caudal length	Dorsal pterygiophores number	Anal pterygiophores number	Total vertebrae number	Precaudal vertebrae number	Caudal vertebrae number	Skull length
	P.4266.27	24	?	2.6	16.9	7	9.9	?	10	30	12	18	7.1
	P.4266.29	23	?	?	?	?	10.3	?	?	?	?	20	?
	P.4266.30	24.4	2	2.7	16.9	6.1	10.8	8	10	29	11	18	7.5
	P.4266.31	24	?	3.4	18.4	7	11.4	?	14	31	11	20	5.6
	P.4266.32	28.2	?	3.9	19.9	7.9	12	?	14	29	10	19	8.3
	P.4266.33	28.9	2.9	3.1	?	?	12.7	8	10	?	?	18	?
	P.4266.35	26.5	?	3.3	18.2	6.6	11.6	?	14	31	11	20	8.3
	P.4266.37	24.2	2.8	4.2	17	6	11	8	14	29	10	19	7.2
	P.4266.38	25	2.6	3.5	18.5	7	11.5	10	14	30	10	20	6.5
	P.4266.39	26.6	4	3.3	18.9	7	11.9	8	14	30	10	20	7.7
	P.4266.40	26.8	2	3.5	19	6.5	12.5	6	13	29	10	19	7.8
	P.4266.43	23.1	3	3.8	16.1	5.1	11	10	12	29	10	19	7
	P.4266.45	28.6	2.6	3.9	?	?	13.4	8	13	?	?	20	?
	P.4266.46	24.1	2.1	2.5	?	?	11.2	8	10	?	?	19	?
	P.4266.47	22.8	2.1	?	?	?	10.3	8	?	?	?	20	?
	P.4266.48	23.5	?	3.1	?	?	11	?	13	?	?	20	?
	P.4266.52	25.8	?	?	18	6.3	11.7	?	?	29	10	19	7.8
	P.4266.53	23.5	2.2	3.4	16.5	6.6	9.9	10	14	30	12	18	7
	P.4266.54	23.2	?	3.5	16.3	6	10.3	?	16	28	10	18	6.9
	P.4266.55	24.2	?	?	17.2	7	10.2	?	?	29	11	18	7
	P.4266.56	24	?	?	17.7	6.7	11	?	?	29	10	19	6.3
	P.4266.57	24.8	?	3	18.1	7	11.1	?	12	30	10	20	6.7
	P.4266.58	23.5	2.1	3.1	17.3	6.9	10.4	10	12	28	10	18	6.2
	P.4266.60	26.1	?	?	?	?	11.9	?	?	?	?	20	?
	P.4266.61	24.2	?	3.6	?	?	11.4	?	12	?	?	20	?
	P.4266.62	24.1	2.8	3.7	?	?	11	8	12	?	?	19	?
	P.4266.65	22.7	?	?	17	6.5	10.5	?	?	30	11	19	5.7
	P.4266.66	30	?	3.9	23.3	9.8	13.5	?	12	29	10	19	6.7
	P.4266.69	28.5	2.7	?	20.8	8	12.8	10	?	29	10	19	7.7
	P.4266.71	26	2.8	?	18.7	6.8	11.9	8	?	30	11	19	7.3
	P.4266.72	22.5	2.5	?	?	?	10.2	10	?	?	?	20	?
	P.4266.74	25.2	2.2	3	19.1	7.6	11.5	8	12	31	11	20	6.1

Species	Specimen	Standard length	Dorsal fin base length	Anal fin base length	Total vertebral length	Precaudal length	Caudal length	Dorsal pterygiophores number	Anal pterygiophores number	Total vertebrae number	Precaudal vertebrae number	Caudal vertebrae number	Skull length
	P.4266.75	32.1	2.4	3.5	24.4	9.8	14.6	8	14	30	11	19	7.7
	P.4266.76	26.7	4.2	3.4	19.3	7.3	12	9	14	31	11	20	7.4
	P.4266.77	24.1	1.8	?	17.9	6.5	11.4	7	?	30	11	19	6.2
	P.4266.78	25.5	2.5	3.6	18	6.7	11.3	10	13	30	11	19	7.5
	P.4266.79	25.8	1.8	2.9	19.2	7	12.2	8	10	30	10	20	6.6
	P.4266.80	25.2	?	3.1	18.7	7.1	11.6	?	14	31	11	20	6.5
	P.4266.82	24.5	1.6	3.2	17.3	7	10.3	6	14	30	11	19	7.2
	P.4266.84	32	3	4.1	23.3	8.5	14.8	8	12	31	11	20	8.7
	P.4266.85	30	3.2	5.6	21.1	8.1	13	8	14	29	11	18	8.9
	P.4266.87	20.7	1.9	2.6	15.7	5.9	9.8	8	12	30	10	20	5
	P.4266.88	26.8	2.9	3.7	19.8	7.8	12	8	12	31	11	20	7
	P.4266.89	24	2.5	3	17	6.5	10.5	10	12	28	10	18	7
	P.4266.95	24.2	2.5	3.4	18.1	7.3	10.8	10	14	31	11	20	6.1
	P.4266.96	33.2	3.2	4.3	23.1	9	14.1	10	12	30	10	20	10.1
	P.4266.97	23.5	2	3.1	?	?	11.3	8	14	?	?	19	?
	P.4266.98	22.8	2.1	3	16.2	5.7	10.5	8	12	29	10	19	6.6
	P.4266.100	25.8	2.4	4.5	18	6.8	11.2	10	13	30	10	20	7.8
	P.4266.101	26.1	2.2	3.8	20.3	8.2	12.1	8	15	31	11	20	5.8
	P.4266.102	23.1	1.7	3.4	16.7	6.2	10.5	8	14	29	10	19	6.4
	P.4266.104	30	3.1	5	?	?	14.2	10	14	?	?	20	?