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Comparative Functional Morphology of Skulls among Japanese Breeds of Domestic Fowls

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The skull of six Japanese fowl breeds, namely, Chabo, Oh-Shamo, Onagadori, Shokoku, Tosajidori, and Totenko, were morphologically compared in this study. The morphological differences in the skull size and shape among the breeds were as follows. 1) Oh-Shamo possessed a wide bill, thick bill tip, small orbits and wide mandibular joint. The characteristics of the bill and mandible were interpreted as functional characteristics to endure the shock of pecking. We suggest that the small orbits and a wide frontal bone help in protection from pecking in games. 2) Chabo possessed a small skull. In terms of shape, this breed possessed relatively large orbits, a wide and high skull and a short bill. The wide and high skull and the short bill formed a circular-shaped face. We propose that these characteristics have led to its characterisation as ornament-type fowl. 3) Totenko, Shokoku, Onagadori and Oh-Shamo possess a long mandible. The long mandible led to an increase in the volume of the oral cavity. The wide resonance space is responsible for the low-frequency voice. The low-frequency crowing of Totenko, Shokoku, Oh-Shamo and Onagadori is a result of the enlarged resonance space created by the long mandible. The orbits of Totenko and Onagadori were larger than those of Shokoku and Oh-Shamo. We suggest that Shokoku possessed the small orbits as a fighting cock. Since Onagadori and Totenko had been bred as ornament-type fowl, they possessed larger orbits.

Key words: Japanese fowl, morphological characteristic, shape, size, skull

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Introduction

Domestic fowls have gained various morphological characteristic as not only as livestock animals but also as companion animals (Frahm and Rehkämper, 1998; Okamoto, 2001; Ichinoe and Kuwayama, 2007; Akishinonomiya and Komiya, 2009; Sheppy, 2011). In Japan, variegated breeds were developed and these were admired for their colour variation, voice and fighting abilities, in the mid-Edo Era (Oana, 1951; Okamoto, 2001; Ichinoe and Kuwayama, 2007; Akishinonomiya and Komiya, 2009). Fighting fowls are highly aggressive and were bred for gambling as a form of entertainment. Long-crowing fowls were selected on the basis of their ability to crow for a longer period of time. Ornament-type fowls acquired colourful feathers or long-tailed feathers for attracting people. Native fowls are called Jidori and their external characteristics are similar to those of the Red Jungle Fowl. These various types of fowls were established and developed before the Meiji period.

Japanese fowls vary not only in external characteristics but also in osteological characteristics. From the report of Hayashi *et al*. (1982), Japanese breeds were categorised into the big-, middle- and small-sized groups on the basis of the skull size, and the smallest breadth between orbits was shown as a remarkable differential characteristic. The size categories of skull were also supported by Samejima *et al*. (1988). Nishida *et al*. (1985) examined whole skeletons and indicated that Japanese breeds were separated into size-based groups and that morphological differences were confirmed in the tibiotarsus, tarsometatarsus and sternum.

The above-mentioned studies showed that Japanese fowls obviously differed in skull size, however, the morphological differences in the skull shape remain unclear. The skeleton morphologically reflects the result of artificial selection driven by assessing not only economical characters for agricultural productions but also by noneconomical characters for spiritual preferences such as a long voice, strong ag-

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gression and external appearances. Since Japanese fowls were selected for fighting fowls, long-crowing fowls and ornament-type fowls, we expected that the functional morphological skull characteristics peculiar to various breeds in their skull could be detected.

Materials and Methods

Specimens

To clarify the relationship between the skull shapes and breed types, the skulls of six breeds, namely, Oh-Shamo, Onagadori, Shokoku, Totenko, Tosajidori and Chabo, were osteometrically compared. The characters of each breed and the reason why we used these breeds are as follows; Oh-Shamo possess a large body and strong combative instinct as a fighting fowl, Chabo is equipped with a small body and colourful feathers as an ornament-type fowl, Totenko possesses the ability to crow for the longest period as a long-crowing and ornament-type fowl, Onagadori acquired longest tail feather as a long-tailed and ornament-type fowl, Shokoku possesses strong aggression, long voice and tail feather and it is considered as an ancestor of Totenko and Onagadori, and Tosajidori is one of the oldest breeds in Japan (Oana, 1951; Okamoto, 2001; Ichinoe and Kuwayama, 2007; Akishinonomiya and Komiya, 2009). It has also been estimated that the feather colour and body size of Tosajidori are similar to those of red jungle fowl. To compare the morphological differences, we used this breed as a control. We used the skulls of these breeds, which were provided by Hiroshima University and Tokyo University of Agriculture. The Nagoya University Museum permitted us to use the other specimens (Table 1). The adult skulls were used in this study. In the unidentified growth stage of specimens, we defined the growth stage by the degree of ossification of skull (Hogg, 1978). The specimens such as over one years old or completed ossification of skull, were defined as the adult (Table 1).

Measurements

The details of measurements are shown in Table 2 and Fig. 1. With regard to size, we compared the measurement values in each breed. With regard to shape, we used measurement ratios which were obtained by dividing the measurement values by geometric means (GM) (Darroch and Mosimann, 1985). We calculated the GM, which consisted of the GLs, GBs and GLmp ($GM = \sqrt[3]{GLs, GBs, GLmp}$).

The GM was considered as an index of the skull size. To establish the measurements, we followed the procedure described by Driesch (1976), Hayashi *et al*. (1982), Samejima *et al*. (1988) and Yasuda (2002). The 28 selected measurements were determined using a caliper, and the values were rounded off to the nearest 0.05 mm (Table 2, Fig. 1).

Analyses

To clarify the morphological characters, we calculated the

Table 1. **Specimens used in this study**

breed	sex	specimen No.	growth stage	donor	depository	breed	sex	specimen No.	growth stage	donor	depository
Onagadori	female	UMUT-14014	adult[1]	TUA	UMUT	Totenko	female	UMUT-14029	adult[1]	TUA	UMUT
Onagadori	female	UMUT-14015	adult[1]	HU	UMUT	Totenko	female	UMUT-14030	adult[1]	TUA	UMUT
Onagadori	female	UMUT-14016	adult[1]	HU	UMUT	Totenko	male	UMUT-14031	adult[1]	TUA	UMUT
Onagadori	male	UMUT-14017	adult[1]	TUA	UMUT	Totenko	male	UMUT-14032	adult[1]	TUA	UMUT
Onagadori	male	NUM-ab1-1202	adult[2]	—	NUM	Totenko	male	UMUT-14033	adult[1]	TUA	UMUT
Oh-Shamo	female	UMUT-14018	adult[1]	TUA	UMUT	Totenko	male	UMUT-14034	adult[2]	HU	UMUT
Oh-Shamo	female	UMUT-14019	adult[1]	TUA	UMUT	Chabo	female	UMUT-14035	adult[1]	TUA	UMUT
Oh-Shamo	female	UMUT-14020	adult[1]	TUA	UMUT	Chabo	female	UMUT-14036	adult[1]	TUA	UMUT
Oh-Shamo	male	UMUT-14021	adult[1]	TUA	UMUT	Chabo	female	NUM-ab1-926	adult[2]	—	NUM
Oh-Shamo	male	NUM-ab1-1230	adult[2]	—	NUM	Chabo	male	UMUT-14037	adult[1]	TUA	UMUT
Oh-Shamo	male	UMUT-14022	adult[1]	TUA	UMUT	Chabo	male	UMUT-14039	adult[1]	TUA	UMUT
Oh-Shamo	unknown	UMUT-14023	adult[1]	TUA	UMUT	Chabo	male	UMUT-14040	adult[1]	TUA	UMUT
Oh-Shamo	unknown	UMUT-14024	adult[1]	TUA	UMUT	Chabo	male	UMUT-14041	adult[1]	TUA	UMUT
Shokoku	female	NUM-ab1-1256	adult[2]	—	NUM	Chabo	male	UMUT-14042	adult[1]	TUA	UMUT
Shokoku	female	NUM-ab1-1255	adult[2]	—	NUM	Chabo	male	NUM-abl1945	adult[2]	—	NUM
Shokoku	male	NUM-ab1-973	adult[2]	—	NUM	Chabo	male	NUM-ab1-922	adult[2]	—	NUM
Shokoku	male	NUM-ab1-1307	adult[2]	—	NUM	Chabo	unknown	UMUT-14043	adult[1]	TUA	UMUT
Shokoku	male	NUM-ab1-1347	adult[2]	—	NUM	Chabo	unknown	NUM-ab1-925	adult[2]	—	NUM
Shokoku	male	UMUT-14025	adult[1]	TUA	UMUT						
Tosajidori	female	NUM-ab1-1336	adult[2]	—	NUM						
Tosajidori	female	UMUT-14026	adult[1]	HU	UMUT						
Tosajidori	male	UMUT-14027	adult[1]	TUA	UMUT						
Tosajidori	male	NUM-ab1-1281	adult[2]	—	NUM						
Tosajidori	unknown	UMUT-14028	adult[1]	TUA	UMUT						

UMUT indicates The University Museum, The University of Tokyo. NUM indicates Nagoya University Museum, Nagoya University. HU indicates Hiroshima University. TUA indicates Tokyo University of Agriculture. adult[1] indicates over one years old. adult[2] indicates completed ossification of skull.

Table 2. **The measurements used in this study**

Abbreviation of measurements	Details	Abbreviation of measurements	Details
GLs	greatest length of skull; protuberantia occipitalis externa - apex praemaxillaris[a, b, c]	BLbt	basal length of the bill tip; most frontal point of the corpus premaxillare - most frontal point of the basal incisura nassle[d]
GLi	greatest length of incisivum; apex praemaxillaris - most aboral point of the processus frontales of the incisivum in the median plane[a, b, c]	CbL	condulobasal length; aboral border of the occipital condyle - apex praemaxiilaris[a, b, c]
BLb	basal length of bill; apex praemaxillaris -most caudal points of the processus maxiallis ossis premaxillaris[d]	GBsb	greatest breadth of the sphenoidal bone; between each most wide point on the limbus sphenoidalis[c]
GLbt	greatest length of bill tip; most frontal point of the premaxillaris - the most frontal point of the nasals[d]	Bpr	breadth between the processus retriangularis; between each point of the processus retroangularis[d]
Hbt	height of bill tip; highest point above the most frontal point of the nasals - lowest point under the most frontal point of the nasals[d]	GLm	greatest length of the mandible; apex to the most aboral point of the mandible[a, b, c]
GLoc	greatest length of orbital cavity; most frontal point of the aucus zygomaticus - most aboral point of the processus frontalis[d]	Leaba	length between the aboral edge of articural bone to the apex; pars symphysialis - condylus musculris mandibularis caudalis[a, b, c]
GLmp	greatest length in the median plane; the basitemporale in the median plane - highest and median point of the braincase[a, b, c]	Lpaa	length between the processus angularis to the apex; apex to the processus angularis[c]
GBbt	greatest breadth of bill tip; most wide breadth in front of the most frontal points of the nasals[d]	Ls	length of the symphesis; between frontal apex of mandible to aboral one[a, b, c]
Lnc	length of the neurocranium; processus frontalis of the paemaxilla - protuberantia occipitalis externa[a, b, c]	Lpapr	length between the processus angularis to processus retroangularis; pcrocessus angularis - processus retroangularis[c]
GBs	greatest breadth of skull; between each point of the processus postfrontalis[a, b, c]	GLabpa	greatest length between the edge of articular bone to the processus angularis[c]
GBnc	greatest breadth of the neurocranium; between each point of the os opistoideus[c]	Lpaps	length between the processus angularis to the aboral edge of the pars symphysialis[d]
SBnc	smallest breadth of the neurocranium; between each point of the os quadratum[c]	GBco	greatest breadth of the condylus occipitalis[d]
SBo	smallest breadth between the orbits; smallest breadth of the pars nasalis of the frontale[a, b, c]	GHfm	greatest height of the foramen magnum[c]
GBb	greatest breadth of the bill; between each point of the caudal edge of the processus maxillaris ossis premaxillaris[d]	GBfm	greatest breadth of the foramen magnum[c]

[a] Driesch (1976). [b] Hayashi *et al*. (1982). [c] Samejima *et al*. (1988). [d] Yasuda (2002).

mean values and standard deviations (SD) of all measurements in each breed. Following this, we performed one-way analysis of variance (ANOVA) to identify differences among breeds. When ANOVA indicated significant morphological differences, it was followed by Tukey- Kramer method for multiple comparisons. Morphological differences were considered significant at a P value of <0.05. Statistical analyses were operated by R (R: A language and environment for statistical computing. URL http://www.R-project.org/). We utilised correlation analysis to examine the relationships between the skull size and shape.

Results

To detect the morphological differences among each breed, we did not separate the sex in each breed. Since the individuals of each breed were few, it was not appropriate to detect the sexual dimorphism. The morphological differences among breeds were confirmed by analysis of the size data from measurement values and the shape data from measurement ratios. The mean values and SDs in all measurement values and measurement ratios of each breed are shown in Tables 3 and 4. Each breed showed differences in morphological characteristics as follows.

Oh-Shamo

The highest measurement values were observed in all measurements (Table 3). The GHfm did not show significant size differences among Onagadori, Shokoku and Totenko (Table 3). In terms of the shape, Oh-Shamo pos-

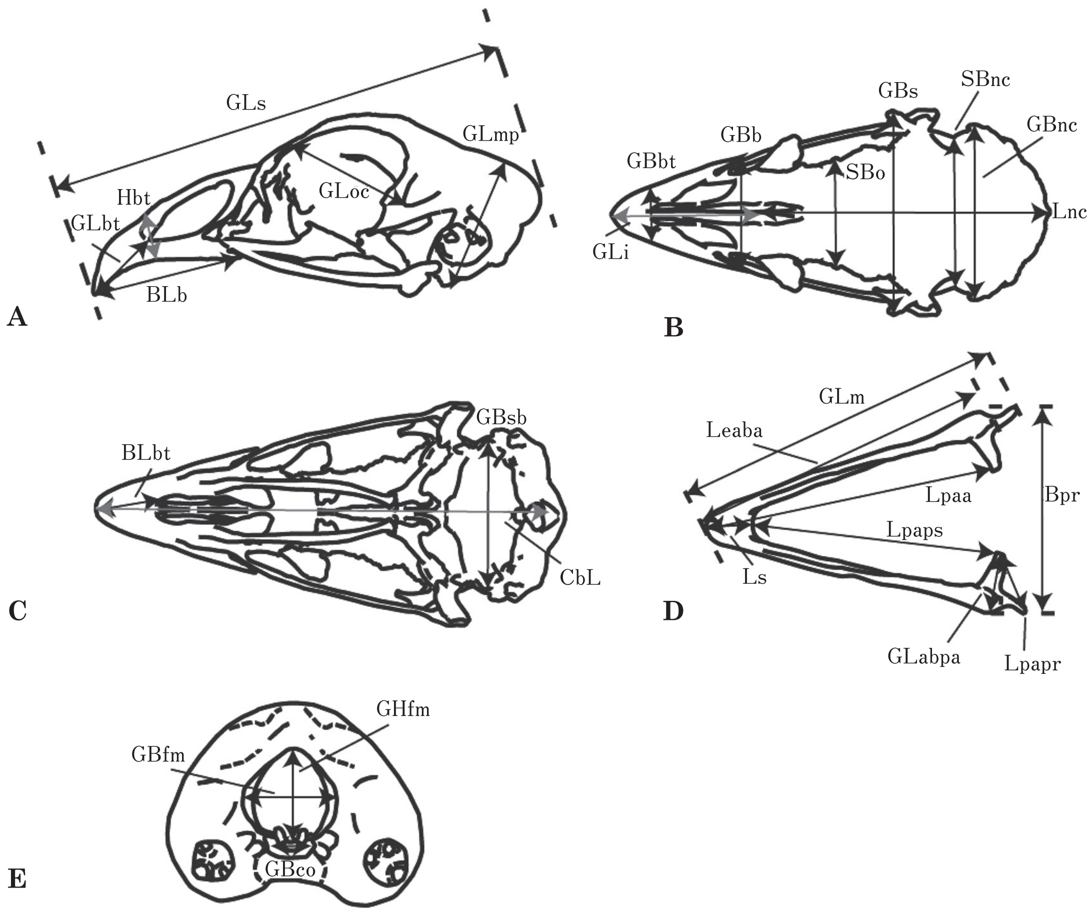

Fig. 1. **The measurements in cranium and mandible.** (A) Cranium of lateral view from left side. (B) Cranium, from dorsal view. (C) Cranium from ventral view. (D) Mandible from dorsal view. (E) Cranium from caudal view. The abbreviated forms were remarked in Table 2.

sessed wider SBo, GBb and GLabpa, lowest height of GLmp and GHfm, thickest Hbt and smaller GLoc. In the Hbt, GLmp, GLabpa and GHfm, we also confirmed the significant differences (Table 4).

Shokoku

The size of Shokoku comparatively ranged between that of Oh-Shamo and Tosajidori (Table 3). The middle values of all measurements, except for GLoc and GBb, were similar to those of Onagadori and Totenko. No definite difference was observed among each breed, except for Oh-Shamo, however, GLoc was relatively smaller (Table 3). According to the ANOVA results, with regard to shape, GLoc was significantly smaller than that of the other breeds, except for Oh-Syamo and Totenko (Table 4). Thus, Shokoku possessed longer GLi, wider GBnc and GBsb, and narrower GBb (Table 4).

Onagadori

All the measurements with regard to size did not show any significant differences in Shokoku and Totenko. All the measurement values were similar to those of Shokoku and Totenko, however, the Lpapr was larger than that of Shokoku and Totenko (Table 3). In terms of measurement ratios, Lpapr and GBfm indicated higher ratios than those of the other breeds (Table 4).

Totenko

Significant size differences were detected in Oh-Shamo, Chabo and Tosajidori in size. Their measurement values were smaller than those of Oh-Shamo and larger than those of Chabo (Table 3). All measurement values were similar to those of Shokoku and Onagadori (Table 3). With regard to shape, the mean ratio of GBnc was lower than that of the other breeds, however, it was not significantly difference (Table 4).

Tosajidori

The size of Tosajidori was similar to that of Chabo. They had smaller values than those of the other breeds in each measurement (Table 3). The measurements with the significant differences between each breed without Chabo were Bpr, GBnc, GBs, GBsb, Leaba, Lpaa, Lpaps and Ls (Table 3). Although similar results were also obtained with regard

Table 3. **Mean values and standard deviations for skull measurement in various breeds**

breed	measurements	GLs	GLi	BLb	GLbt	Hbt	GLoc	GLmp	GBbt	Lnc	GBs
	comparing pair with significant difference	AEFGH IJLMO	AEFGH IJLMO	AEFGH ILMO	ACEFG HILMO	AFGHI	AFGHI	AEFGH ILMO	AFGHI	ACEFG HILMO	ACEFG HIJLMO
Onagadori	mean value	67.19	34.45	24.01	13.10	5.75	21.11	20.83	8.51	37.07	29.14
	standard deviation	4.81	2.53	2.43	1.20	0.79	1.01	0.95	0.63	3.41	2.25
Oh-Shamo	mean value	85.86	45.37	30.86	16.53	8.46	24.49	25.40	11.77	46.31	37.83
	standard deviation	6.39	4.50	2.61	1.25	0.92	1.88	1.37	2.10	2.82	1.84
Shokoku	mean value	67.27	35.96	23.87	12.54	5.56	18.91	20.31	8.70	36.14	29.20
	standard deviation	5.10	3.31	2.40	1.54	0.89	2.60	1.46	1.33	2.67	2.44
Tosajidori	mean value	58.26	28.78	20.38	10.67	4.87	18.32	18.76	7.45	32.32	25.39
	standard deviation	2.77	0.99	1.16	0.69	0.77	0.45	0.47	0.32	1.19	1.51
Totenko	mean value	67.73	34.98	25.07	13.29	5.77	20.91	21.16	9.03	37.10	30.13
	standard deviation	5.66	3.45	2.08	1.14	1.04	1.21	1.32	0.71	2.89	2.13
Chabo	mean value	57.67	28.82	20.26	10.40	5.08	19.06	18.54	7.96	32.11	25.58
	standard deviation	3.99	2.06	1.31	0.79	0.56	0.83	0.76	0.59	1.30	1.15

breed	measurements	GBnc	SBnc	SBo	GBb	BLbt	CbL	GBsb	Bpr	GLm	Leaba
	comparing pair with significant difference	ACEFG HIJLMO	AFGHI LO	AFGHI	AFGHI	AEFGH ILMO	ACEFG HILMO	ACEFG HIJLMO	ACEFG HIJLMO	AEFGH ILO	ACEFG HIJLMO
Onagadori	mean value	25.64	22.60	13.89	12.92	11.98	61.84	19.87	43.40	29.38	54.06
	standard deviation	1.75	1.22	2.20	1.91	0.83	4.60	1.19	6.60	5.18	3.82
Oh-Shamo	mean value	32.48	28.37	19.80	19.43	14.85	78.29	25.03	52.60	39.33	70.00
	standard deviation	2.02	1.42	1.43	1.49	0.97	5.84	1.50	4.40	3.30	5.70
Shokoku	mean value	25.89	22.98	13.70	13.73	11.18	60.73	20.28	40.33	28.80	53.25
	standard deviation	1.52	1.58	2.01	2.46	1.63	4.72	1.01	2.98	2.68	4.20
Tosajidori	mean value	22.66	20.88	12.22	12.25	10.03	52.72	17.18	33.52	24.95	45.27
	standard deviation	1.15	0.75	1.46	0.82	0.65	3.28	0.79	1.20	0.97	1.49
Totenko	mean value	25.65	22.73	14.58	13.86	12.20	62.08	20.39	41.58	29.52	55.13
	standard deviation	2.11	1.87	1.42	2.09	0.89	5.34	2.01	4.16	2.35	4.13
Chabo	mean value	22.46	20.69	12.53	12.70	9.60	51.60	16.85	33.08	24.58	44.99
	standard deviation	1.00	0.76	2.05	1.17	0.93	2.94	0.92	1.35	1.63	1.78

breed	measurements	Lpaa	Ls	Lpapr	GLabpa	Lpaps	GBco	GHfm	GBfm	GM
	comparing pair with significant difference	ACEFG HIJLMO	ACEFG HIJLMO	ACEFG HIMO	ACEFG HIMO	ACEFG HIJLMO	AFGHI	EGIJL	ACEFG HILO	ACEFG HIJLMO
Onagadori	mean value	49.31	49.11	9.29	11.12	9.66	3.22	6.25	7.36	34.42
	standard deviation	3.59	3.36	1.13	1.43	0.81	0.48	0.57	0.60	2.17
Oh-Shamo	mean value	63.06	62.74	10.49	15.24	13.69	4.54	6.46	8.31	43.52
	standard deviation	5.40	4.97	0.78	1.32	0.97	0.31	0.63	0.53	2.36
Shokoku	mean value	48.43	48.11	8.27	10.57	9.48	3.42	6.48	6.89	34.17
	standard deviation	3.89	3.48	0.50	1.20	1.01	0.37	0.71	0.56	2.62
Tosajidori	mean value	40.94	40.57	7.46	8.97	7.96	2.93	5.28	6.24	30.26
	standard deviation	1.52	1.68	0.50	0.46	0.60	0.34	0.26	0.33	0.99
Totenko	mean value	50.03	49.63	8.48	10.72	9.81	3.34	5.71	7.05	35.08
	standard deviation	3.90	4.55	0.73	0.54	0.85	0.28	0.85	0.54	2.45
Chabo	mean value	40.50	40.07	7.22	9.31	8.18	3.01	5.28	6.00	30.14
	standard deviation	1.58	1.66	0.50	0.45	0.46	0.32	0.44	0.38	1.35

Each alphabet indicates comparing pair with significant difference as follows; [A] Onagadori - Oh-Shamo, [B] Onagadori - Shokoku, [C] Onagadori - Tosajidori, [D] Onagadori - Totenko, [E] Onagadori - Chabo, [F] Oh-Shamo - Shokoku, [G] Oh-Shamo - Tosajidori, [H] Oh-Shamo - Totenko, [I] Oh-Shamo - Chabo, [J] Shokoku - Tosajidori, [K] Shokoku - Totenko, [L] Shokoku - Chabo, [M] Tosajidori - Totenko, [N] Tosajidori - Chabo and [O] Totenko - Chabo.

to shape, the mean ratios of BLb, GBb, GBbt, GBco, GBs, GLabpa, GLi, GLoc, Hbt and Lpapr were lower than those of Chabo (Table 4).

Chabo

All measurement values were smaller than those of each breed, except for Tosajidori (Table 3). Comparison of the mean values of each shape measurement showed longer GLoc and wider GBs, GBb and GBco than those of Tosajidori (Table 4). In terms of the significant coefficient, they indicated lower ratios of Leaba and Lpaa than those of all breeds, except for Tosajidori (Table 4).

Table 4. **Mean values and standard deviations for skull measurement ratio in various breeds**

breed	measurements	GLs	GLi	BLb	GLbt	Hbt	GLoc	GLmp	GBbt	Lnc	GBs
comparing pair with significant difference		—	gijl	—	eio	fghi	abijl	agijl	—	—	—
Onagadori	mean value	1.95	1.00	0.70	0.38	0.17	0.61	0.61	0.25	1.08	0.85
	standard deviation	0.03	0.02	0.04	0.03	0.01	0.02	0.01	0.01	0.05	0.02
Oh-Shamo	mean value	1.97	1.04	0.71	0.38	0.19	0.56	0.58	0.27	1.06	0.87
	standard deviation	0.06	0.06	0.03	0.01	0.02	0.01	0.01	0.05	0.02	0.02
Shokoku	mean value	1.97	1.05	0.70	0.37	0.16	0.55	0.59	0.25	1.06	0.85
	standard deviation	0.02	0.04	0.04	0.03	0.02	0.04	0.01	0.02	0.02	0.01
Tosajidori	mean value	1.92	0.95	0.67	0.35	0.16	0.61	0.62	0.25	1.07	0.84
	standard deviation	0.05	0.02	0.02	0.02	0.02	0.01	0.02	0.01	0.02	0.03
Totenko	mean value	1.93	1.00	0.71	0.38	0.16	0.60	0.60	0.26	1.06	0.86
	standard deviation	0.04	0.06	0.02	0.01	0.02	0.01	0.01	0.02	0.02	0.02
Chabo	mean value	1.91	0.96	0.67	0.35	0.17	0.63	0.62	0.26	1.07	0.85
	standard deviation	0.06	0.05	0.04	0.02	0.01	0.04	0.01	0.02	0.03	0.02

breed	measurements	GBnc	SBnc	SBo	GBb	BLbt	CbL	GBsb	Bpr	GLm	Leaba
comparing pair with significant difference		—	cegimo	—	a	—	ei	l	cei	i	egilo
Onagadori	mean value	0.75	0.66	0.40	0.37	0.35	1.80	0.58	1.26	0.85	1.57
	standard deviation	0.02	0.02	0.05	0.03	0.02	0.03	0.01	0.18	0.12	0.04
Oh-Shamo	mean value	0.75	0.65	0.46	0.45	0.34	1.80	0.58	1.21	0.90	1.61
	standard deviation	0.01	0.01	0.03	0.03	0.01	0.06	0.02	0.04	0.04	0.06
Shokoku	mean value	0.76	0.67	0.40	0.40	0.33	1.78	0.59	1.18	0.84	1.56
	standard deviation	0.02	0.01	0.04	0.05	0.03	0.03	0.02	0.02	0.03	0.02
Tosajidori	mean value	0.75	0.69	0.40	0.40	0.33	1.74	0.57	1.11	0.82	1.50
	standard deviation	0.02	0.01	0.04	0.02	0.01	0.07	0.01	0.02	0.02	0.01
Totenko	mean value	0.73	0.65	0.42	0.39	0.35	1.77	0.58	1.18	0.84	1.57
	standard deviation	0.02	0.02	0.03	0.05	0.02	0.04	0.02	0.06	0.03	0.04
Chabo	mean value	0.75	0.69	0.42	0.42	0.32	1.71	0.56	1.10	0.82	1.49
	standard deviation	0.01	0.02	0.06	0.03	0.03	0.05	0.02	0.04	0.04	0.05

breed	measurements	Lpaa	Ls	Lpapr	GLabpa	Lpaps	GBco	GHfm	GBfm
comparing pair with significant difference		cegilo	cegilo	ae	afghi	afghi	—	afi	a
Onagadori	mean value	1.43	1.43	0.27	0.32	0.28	0.09	0.18	0.21
	standard deviation	0.03	0.03	0.03	0.02	0.01	0.01	0.02	0.02
Oh-Shamo	mean value	1.45	1.44	0.24	0.35	0.31	0.10	0.15	0.19
	standard deviation	0.06	0.05	0.01	0.02	0.01	0.00	0.02	0.01
Shokoku	mean value	1.42	1.41	0.24	0.31	0.28	0.10	0.19	0.20
	standard deviation	0.03	0.02	0.01	0.01	0.01	0.00	0.02	0.01
Tosajidori	mean value	1.35	1.34	0.25	0.30	0.26	0.10	0.17	0.21
	standard deviation	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Totenko	mean value	1.43	1.41	0.24	0.31	0.28	0.10	0.16	0.20
	standard deviation	0.03	0.06	0.01	0.02	0.01	0.01	0.03	0.01
Chabo	mean value	1.34	1.33	0.24	0.31	0.27	0.10	0.18	0.20
	standard deviation	0.05	0.05	0.02	0.01	0.01	0.01	0.01	0.01

Each alphabet indicates comparing pair with significant difference as follows; [a] Onagadori - Oh-Shamo, [b] Onagadori - Shokoku, [c] Onagadori - Tosajidori, [d] Onagadori - Totenko, [e] Onagadori - Chabo, [f] Oh-Shamo - Shokoku, [g] Oh-Shamo - Tosajidori, [h] Oh-Shamo - Totenko, [i] Oh-Shamo - Chabo, [j] Shokoku - Tosajidori, [k] Shokoku - Totenko, [l] Shokoku - Chabo, [m] Tosajidori - Totenko, [n] Tosajidori - Chabo and [o] Totenko - Chabo. – signified that every pair shows no significant difference.

Discussion

The Functional Morphology of the Skull of Oh-Shamo

This study clarified that Oh-Shamo is equipped with a wider bill, thicker bill tip, smaller orbits and wider mandibular joint and frontal bone than the other breeds (Tables 3 and 4). Bock (1966) indicated that an impact force is received by the quadrate in birds. He also suggested that a long and wide bill is adapted to endure the shock of drill in woodpeckers (Bock, 1999). Oh-Shamo frequently uses its bill for attacking in games. When it attacks with its bill, the bill needs to endure the impact. The wide bill shown in GBb and Hbt and wide mandibular joint seen in GLabpa and Lpapr were interpreted as the functional characteristics for enduring the shock when pecking during a fight. Bock (1966) remarked that the impact force acts especially on the bill tip. The decurved bill tip was interpreted as a suitable characteristic for enduring the impact force (Bock, 1966). We did not measure the bill tip curvature, however, a higher ratio of Hbt was observed in Oh-Shamo (Table 4). The thicker bill tip is also a functional characteristic for enduring the shock.

Dundes (1994) mentioned that when fighting cocks injured their eyes in combat, their eyelid were sewed up and continued the battle. The eye is considered as the weak point in fight. We suggest that the smaller orbits decrease the exposed area of eye and the wider frontal bone contribute to protection from pecking by covering the eye.

The Motivation of the Selection in Ornament-type Fowls

All measurements of Chabo and Tosajidori were smaller than those of the other breeds (Table 3). With regard to shape, they possess a wider and higher skull, shorter bill and larger orbits than the other breeds (Table 4). With regard to mean measurement ratios, Chabo was equipped with a wider skull and larger orbits than Tosajidori (Table 4). In the dorsal and caudal views, a wide skull shows a circle-like silhouette. The higher skull and shorter bill indicate the circular-like outline in lateral view. Chabo and Tosajidori possessed similar GM, however, Chabo was equipped with a wider skull than Tosajidori in terms of measurement ratios. In summary, Chabo have a small-sized skull and the circular-like silhouette of the skull showed larger orbits.

A head shape such as a circular face attracts humans (Alley, 1981). Hildebrandt and Fitzgerald (1979) reported that people are attracted to big eyes in humans. Japanese find small objects to be cute (Nittono, 2009). We propose that people also preferred Chabo, which has a circular small skull and big orbits, as an ornament-type breed. In Chabo, poultry breeders put high value on external characteristics of the head such as an attractive face.

Characteristics such as big eyes and a round face are one of the "baby schemas" (Lorenz, 1943). "Baby schemas" induce motivation and behaviour for approach and caregiving (Glocker *et al*., 2009). Dogs and cats, which possess infant characters, are preferred (Archer and Monton, 2011; Little, 2012). The observed characteristics such as larger orbits and a circular-like silhouette in the present study are estimated to be the functional morphological characteristics for acquiring caregiving in ornament-type fowls.

The Morphological Characters of the Bill and Orbit among the Oh-Shamo, Onagadori, Shokoku and Totenko

Kuwayama *et al*. (1996) studied the duration and the pitch of crowing and reported that Totenko, Shokoku, Onagadori and Oh-Shamo produce a low voice. In this study, we noticed that Totenko, Shokoku, Onagadori and Oh-Shamo possess a larger mandible than Chabo and Tosajidori (Tables 3 and 4). The large mandible led to an increase in the oral cavity space. As the resonance volume increases, the frequency of sound becomes lower (Stevens, 1998). Palacios and Tubaro (2000) indicated that the longer beak contribute to the lower acoustic frequencies of the song in woodcreepers. We suppose that the presence of a large mandible increases the resonance volume. The wide resonance volume contributes to a low voice in these breeds.

Totenko and Onagadori possess larger orbits than Shokoku and Oh-Shamo (Table 4). Akisinonomiya and Komiya (2009) described that Shokoku is characterized by long crowing abilities, a strong aggressive instinct and a long tail feather and has been bred as a fighting cock. Totenko and Onagadori have been bred as ornament-type fowls and not as fighting cocks. Since Shokoku has been bred as a fighting cock, it has retained small orbits such as that observed in Oh-Shamo. Onagadori and Totenko have larger orbits since they have been bred as ornament-type fowls.

The Relationships of Size between Orbit and Foramen Magnum

We observed a smaller orbit and foramen magnum in Oh-Shamo (Table 4). The size of the foramen magnum and brain shows a positive correlation in birds (Mlikovský, 2003). In addition, the brain size is also positively correlated with the eye size in birds (Burton, 2008). Since Oh-Shamo possesses smaller orbits and foramen magnum, we estimate that its brain size is presumably small. GLmp and SBnc are interpreted to be indices of the brain size. The ratio of GLmp and SBnc was undoubtedly smaller than that of the other breeds (Table 4). Observed characteristics such as larger orbits and larger SBnc and GLmp in Chabo (Table 4) suggest that its brain may be larger, however, its foramen magnum was not larger than that of the other breeds except for Oh-Shamo (Table 4). The foramen magnum is surrounded by basioccipital, exoccipital and supraoccipital bones (Jollie, 1957; Yasuda, 2002). Hogg (1978) reported that the articulation of basioccipital, exoccipital and supraoccipital bones is earlier than that of the facial bone in domestic fowl. We suggest that the early articulation of occipital bones restricts the size of the foramen magnum.

Although the ratio of GBnc and SBnc of Onagadori was not larger than that of the other breeds, its GBfm was the largest (Table 4). A dorsal notch or an extension in the foramen magnum is recognised as occipital dysplasia (Bagley *et al*., 1996). The dorsal notch of the foramen magnum is caused by the incomplete ossification of the ventromedial part of the supraoccipital bone (Watson *et al*., 1989). We suggest that the large foramen magnum in Onagadori is influenced by the imcomplete ossification of the supraoccipital bone.

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